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HERBERTIA

International Journal of the American Plant Life Society, devoted to the increase and diffusion of knowledge on bulbous plants and petaloid monocot families, especially the Amaryllidaceae.

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The contributed papers to the 1989 Irvine Symposium have finally all been received from the authors and are published in this combined issue for 1989.

R. Mitchel Beauchamp, Editor

Cover: Leucocoryne purpurea.

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PROCEEDINGS

International Symposium on Bulbous and Cormous Plants
Irvine, California, U S A

24 to 26 February 1989

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THE PROBLEM OF WILD-COLLECTED BULBS FROM THE PERSPECTIVE OF THE NATURAL RESOURCES DEFENSE COUNCIL

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ON behalf of the Natural Resources Defense Council (NRDC), I have sought to improve conservation of plant species *in situ* for the past decade or more. Overcollecting for the horticultural market is one threat to plant species which we attempt to curb. Beginning in 1986, I expanded this work to include "bulbs". NRDC's concern about trade in bulbous species was aroused by a report by Dr. Ekim, a Turkish botanist, and correspondence from other plant conservationists concerned about a greater emphasis on species bulbs in an increasing number of catalogs.

Americans plant over a billion bulbs each year. NRDC recognizes that most of these are hybrids produced in nurseries. However, some are plants which have been taken from the wild. Unfortunately, it is very difficult for the buyer or researcher to determine which are which. Dealers often handle both wild and propagated plants, but rarely identify the origins of particular bulbs.

Worse, some dealers have begun making reassuring statements that their bulbs were obtained from "commercial sources" or were "nursery grown" when our evidence indicates that they were taken from the wild. Bulbs collected systematically in Turkey and other countries are certainly from "commercial sources" at the same time as they are of wild origin. Similarly, standards for declaring a plant to be "nursery grown" which may be adequate for ensuring freedom from pests or ease of establishment do not address the issue of concern here—that the bulb or corm was originally taken from the wild.

SOURCES OF INFORMATION

NRDC began its study in 1986 by surveying 25 catalogs which offer bulbs. We also analyzed the available literature, including a study of Turkish exports of *Cyclamen* by TRAFFIC/NETHERLANDS; a study of Turkish export data for 1986 by Michael Read of Fauna and Flora Preservation Society, U.K.; and a study of 1985 orchid trade data by Drs. Linda McMahan and Kerry Walter of the Center for Plant Conservation. I also reviewed U.S. plant import data contained in permits issued in compliance with the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); these are on file with the U.S. Fish and Wildlife Service. Another source is records of phytosanitary inspections compiled by the Animal and Plant Health Inspection Service (APHIS) for the period 1985-1988. Finally, I have written to local botanists in Turkey, India, South Africa, and South America.

Our work proceeds in close coordination with TRAFFIC (the trade-monitoring branch of World Wildlife Fund), the Garden Club of America, and others.

Mike Read will discuss some recent European trade data and the results of his own research into the trade in Turkey and Iberia. I will proceed with a brief overview of what we

know about some bulb groups, particularly their market in the United States as indicated by the 1986 catalog survey.

AMARYLLIS FAMILY

Galanthus

Turkey has exported over 175 million *Galanthus*, primarily *G. elwesii*, during the past 5 years (Read). In 1986, these exports reached 38.6 million; in 1987, they declined somewhat to 30 million. A second species, *G. ikariae* var *latifolius*, is also exported. These exports are about four times the quantity recommended by Dr. Ekim, a Turkish botanist who has done field research on the bulbs.

Snowdrops are very popular in the United States. Of 25 catalogs surveyed, at least nine sold some type of snowdrops. Three sold *G. elwesii* specifically. According to Sara Oldfield, the Netherlands' exports of the genus to the United States has increased from 2.2 million in 1985 to 4 million in 1987; they are primarily of wild origin.

Narcissus

According to Read, the popular *N. triandrus* is wild-collected. Of the 25 catalogs, 6 sold *N. triandrus* var. *albus*, 2 *concolor*.

According to the European botanists and participants at the International Bulb Symposium, *N. bulbocodium* var. *conspicuus* is propagated to some extent in the Netherlands. However, Read observed collection of this species in Portugal. *N. bulbocodium* was sold by 5 catalogs in our survey.

Sternbergia

Turkish exports exceed 1 million in past 5 years, whereas Ekim has recommended no exports In our survey, 5 or 6 nurseries sold *Sternbergia*.

LILY FAMILY

Erythronium

NRDC is concerned about trade in the North American species; all except the hybrid, "Pagoda", are wild-collected. This genus is sold by only 1 or 2 of the 25 "bulb" catalogs, but more than 7 of the 46 "wildflower" catalogs also surveyed by NRDC in 1986. According to Oldfield, *Erythronium japonicum* is also probably wild.

Trillium

This genus is among the most popular in the trade. Unfortunately, these plants are almost certainly from the wild. No nursery is propagating the large *T. grandiflorum* in commercial quantities, but it was offered by 13 of 46 "wildflower" catalogs.

ORCHID FAMILY

Cypripedium

Among the North American species, there is no commercial propagation of the most popular

species, *C. acaule*; little, if any, of other species. *C. acaule* was sold by 8 "wildflower" catalogs.

Bletilla

This is one of the most heavily traded orchid genera. According to CITES data (which almost certainly understate the actual trade), in 1985, Japan imported 85,000 of the genus (55,000 *B. yunnanensis*, 23,000 *B. ochracea*) from China, exported 61,000 (*striata*) to The Netherlands.

The U.S. is also a major importer. In 1986, we imported from Japan 140,200 plants of the genus. Of these, 105,000 were *B. striata*, 30,000 *B. hyacinthina*, 5,000 *B. alba*. In 1987, this fell to 76,600 *Bletilla*, in 1988 to 52,000 plus one shipment of unknown size.

Until recently, these plants were believed to be propagated. However, British botanist Sara Oldfield recently visited Japan and now raises doubts about this claim. Certainly the plants imported from China are of wild origin.

Worse, some of the species involved are rare. *B. striata* is among 50 Japanese orchids listed in Red Data Book as threatened by overcollecting.

Habenaria from Asia

This is another genus about which concerns have been raised recently. Again, Oldfield visited a Japanese exporter and found no evidence of propagation. The U.S. imported 25,000 of the genus in 1985, another 30,000 in 1987.

Several *Habenaria* species are among 50 Japanese orchids listed in Red Data Book as threatened by overcollecting.

PRIMROSE FAMILY

Cyclamen

All researchers are most concerned about trade in the uncommon *C. mirabile*, which is sometimes exported from Turkey as *C. purpurascens* or *europeanum*.

In our 1986 catalog survey, 6 offered *Cyclamen* species: 5 sold *C. coum*, 5 *C. neapolitanum (hederifolium)*, 4 *C. cilicicum*, 2 *C. purpurascens*. Most were imported through the Netherlands—according to Oldfield, 31,000 in 1985, 143,000 in 1986, and 69,500 in 1987. One dealer imported 86,400 directly from Turkey in 1987. Apparently none was imported directly in 1988. U.S. dealers have imported bulbs from Turkey in earlier years, but we cannot determine the genus or species. At least one U.S. nursery propagates species *Cyclamen*.

RANUNCULACEAE

Anemone

Turkey has exported 35 million over the past 5 years, primarily *A. blanda*. Recent exports of 6.4 million in 1986, 7.5 million in 1987 are within the quota suggested by Dr. Ekim.

According to participants in the International Bulb Symposium, large quantities of *A. blanda* are propagated in the Netherlands. Oldfield reports that Dutch exports to the United states have risen from 32 million in 1985 to 47.7 million in 1987. We do not yet know the proportion of this trade made up by wild Turkish corms.

In the catalog survey, 11 sold *A. blanda*, at least 9 sold other types.

Eranthis

Turkey has exported 60 million over the past 5 years. In 1986, exports reached 13.1 million—one-third over Dr. Ekim's suggested quota. In 1987, exports fell to 10 million, the suggested level.

In our catalog survey, 7 sold *E. hyemalis*, 3 sold *E. cilicia*, 2 sold unspecified members of the genus. According to Oldfield, the Netherlands has exported annually between 600,000 and 700,000 *Eranthis* to the United States; these corms are primarily of wild origin. In 1987, one American dealer imported 155,000 *Eranthis* directly from Turkey. Again, we cannot determine the species for bulb imports from Turkey in other years.

According to data compiled by APHIS, bulb imports from Turkey declined precipitously in 1988.

Turkey: 1985 4,979 kg; no genus or species given
1986 584,462 bulbs; no genus or species given
1987 86,400 *Cyclamen*; 155,000 *Eranthis*
1988 6,525 unidientified bulbs—no *Cyclamen*

According to APHIS, these figures reflect a real decline, not a statistical anomaly resulting from a change in how APHIS handles Turkish plant exports.

We are concerned about recent increases in imports from other countries where the likelihood of propagation is not great. India went from 100,000 bulbs in 1985 to over 1 million in 1987, then fell back to 250,000 in 1988. The records report the genera for about half the imports in 1988:

1985 100,061 bulbs; no genus or species given
1986 132,900 bulbs; "
1987 1,035,600 bulbs; "
1988 101,150 unidentified; 155,000 named:
Achimenes 45,000
Amorphophallus 2,000
Crinum 1,500
Curcuma 2,500
Eucharis 6,000
Globba 4,000
Gloriosa 8,500
Haemanthus 3,500
Zephyranthes 80,000

Mike Read believes these bulbs are probably wild-collected. I am seeking further information.

Imports from Swaziland have also increased rapidly from only 300 bulbs in 1986 to over 1 million in 1988.

1986 300 bulbs; no genus or species given
1987 408,023 bulbs; "
1988 1,096,034 + 295kg; "

While officials of APHIS say that this increase is made up primarily of propagated *Amaryllis* shipped via Swaziland in order to avoid our trade ban with South Africa, South African

botanists have expressed concern about these data. Read notes that this increase coincides with an increased number of *Amaryllis* species becoming available on the market. Participants in the International Bulb Symposium confirm that the major South African exporter of *Amaryllis* has moved his facilities to Swaziland in order to avoid the trade ban.

We are also concerned about imports from Hong Kong, Peoples Republic of China, and Taiwan. Often no genera are given. Indeed, sometimes one cannot determine which is the exporting country. All three are believed to traffic in rare and illegally obtained plants.

PR China:	1985	1,500 unnamed bulbs; 1,200 *Narcissus*; 8,000 *Lycoris*
	1986	796 unnamed bulbs
	1987	304 " "
	1988	2,000 " + 600 lbs *Narcissus*
Hong Kong	1985	500 unnamed bulbs; 1,700 *Narcissus*
	1987	13,150 unnamed bulbs
	1988	5,040 " "
Taiwan	1986	400 unnamed
	1988	2,000 " , to date
"China"	1986	10,000 unnamed

SUPPORTING ACTIVITIES

NRDC has made a major effort to inform gardeners about the probably wild origin of some plants offered for sale so that they may make an informed decision. I have written several articles, most recently one appearing in *Wildflower*, the new journal of Mrs. Lyndon Johnson's National Wildflower Research Center. NRDC will also have a display at the New York Flower Show which will include overcollecting as one issue. Still to appear is a "debate" on trade in *Narcissus* in *Green Scene*, the publication of Pennsylvania Horticultural Society. Finally, NRDC, Garden Club of America, and World Wildlife Fund plan to publish a joint booklet on the plant trade. In addition, the issue has generated considerable media interest.

Finally, we are also trying to promote "farming" of bulbs in their countries of origin as a long-term solution to the problem. I have suggested this approach to an official of the Turkish Embassy and a World Bank environmental officer, as well as to a representative of the Dutch bulb exporters.

We have also begun a dialogue with some U.S. dealers to encourage more responsible marketing and voluntary decisions not to sell the most vulnerable species.

NRDC continues to study the trade in wild bulbs. Your comments are welcome. NRDC is a non-profit membership organization dedicated to securing a safer and healthier environment through scientific research and legal action.

OVER-EXPLOITATION OF WILD BULBS BY THE HORTICULTURAL TRADE

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THE trade in bulbs is centuries old. Tulips taken back home from Istanbul by the ambassador of Ferdinand I were in flower in Augsburg in 1559. Between 1700 and 1730, rare forms could fetch '500-1,000' gold coins. This trade has waxed and waned over the years, but investigations have now exposed that in the last 15 years imports of wild bulbs have reached enormous and frightening proportions. It is now known that in the last 10 years alone, Turkey has exported, among a list that would fill many pages of a mail-order catalog, or many feet of supermarket shelf-space, 71 million anemones, 20 million cyclamens, 62 million summer snowflakes (*Leucojum*) and 111 million winter aconites (*Eranthis*). The export of snowdrops alone has risen to over 30 million a year. Turkey appears to be by far the greatest source of wild collected bulbs, but it is by no means the only country losing its wildflowers to the trade. The exploitation is occurring from Canada to India and from Portugal to Japan.

Why then has there been this upturn in a completely unnecessary and damaging trade?

First, the discovery of species suitable for Western gardens has not always led to propagation of these species in the nurseries and greenhouses of the horticultural trade, simply because, for some, gardening is a business where short-term profit outweighs other considerations. In other words, if a marketable species is available from the wild at a lower cost than that from artificial propagation, then the wild 'supply' can be exhausted first regardless of the consequence.

Second, the millions of gardeners who buy these wild-collected plants are neither aware of their origin nor of the low quality and unhealthy nature of the plants they are buying.

Third, the horticultural world is always searching for novelty. Ironically the plant breeders' efforts have produced larger and bolder garden hybrids and cultivars that are increasingly inappropriate to the average garden, which shrinks in size with each passing year. The alternative source of novelty is, of course, nature.

THE CHAIN OF TRADE

The pathway of trade that leads, for instance, from a Turkish villager to a Western gardener is complicated and has taken a lot of unravelling. Bulbs can often change hands five or six times along the way. The summary given here is an example of the type of route taken for one of those species collected in enormous quantities for large commercial enterprises and should not be taken to hold true for all cases, least of all for the very rarest species most persistently sought by specialist collectors.

In the village of Bayir, near Marmaris on Turkey's southwestern coast, collecting is organized by Nazmi Kalayci, a local farmer who started collecting *Cyclamen* in 1980. For him and his fellow villagers, the flowers are a welcome free harvest. The ready market for *Cyclamen* bulbs provides a much-needed means of increasing their meager income. Although Nazmi has managed to uproot as many as 1,000 bulbs from the steeply sloping, stony soil around his village in a single day, the total is usually far more modest. During the plants'

flowering season many members of the village community are involved and 10-15 tons of bulbs have been collected around Bayir in a single season. While in the last four years Nazmi has been able to increase the price they sell the bulbs for tenfold, this difference is more than accounted for by massive inflation. It works out at less than one cent per Cyclamen and is back-breaking and sometimes dangerous work. A letter from a villager who lives on the slopes of Mount Anamas in Beysehir-Sarkikaraagac (southern Turkey) describes how in recent years the snowdrop bulbs collected around his village have become restricted to rough and dangerous slopes and how many accidents have been occurring. He expressed the villagers' fears that in the future lives might be lost.

The Turkish traders send out representatives to travel from village to village buying large numbers of a mixture of species. The villagers of Bayir sell their bulbs to an employee of the largest Turkish bulb-export companies,"Marla", based near Istanbul. These wild bulbs are brought together to be sorted for size and species, cleaned and stored, ideally dry and cold, in large warehouses. Sometimes storage conditions leave a lot to be desired and many wild bulbs die from desiccation or rotting while in storage.

Dutch buyers from many of the famous bulb houses in Holland visit their Turkish contacts in late spring and early summer and buy up consignments of many species. Prices vary with species and age of the bulbs; snowdrops make roughly $35/1,000, cyclamens make $155/1,000.

Bulbs are transported right across Europe on large lorries to their destinations, the Dutch bulb companies, which are ready to rapidly sort, pack and sell them again. Very few appear in the enormous Dutch horticultural auctions, generally buyers are already lined up. Those bulbs destined to be re-exported have already been ordered by retailers and wholesalers in the United Kingdom, United States and many other countries and will be transported with much greater quantities of hybrids and cultivars produced by the Dutch growers. In the United Kingdom many of the wild bulbs will appear in their Dutch packets in garden centers and small retail outlets. Many more, having arrived in bulk from Holland, are packaged by UK-based wholesalers and re-sold to large garden centers and supermarkets chains. Many others will appear in the pages of mail-order catalogues.

And so it is that western gardeners will pick up, buy and plant endangered, but colorfully marketed wild plants from the meadows, mountain pastures and woodlands of countries thousands of miles away.

The labelling 'Produce of Holland' serves to complete the deception. Worse still the utterly fraudulent 'Grown in Holland' continues to appear on packets of rare Turkish bulb species which have even been banned from export Turkey.

TRADE DATA

Trade data have proven difficult to compile for a variety of reasons. The wide geographic area involved and 'commercial confidentially' have caused problems, so the information presented here has been drawn from wide and disparate sources. Nevertheless, considerable effort has been made to ensure its accuracy.

A. Where do the bulbs come from?

Research has so far produced evidence that within the last decade wild-bulbs are being commercially exported from at least Afghanistan, Chile, Hungary, Iran, Italy, Japan, Nepal, Pakistan, Portugal, Saudi Arabia, Turkey and the United States. The list is almost certainly incomplete. Most certainly the very rarest species and forms are being arduously sought out

and collected by thousands of specialist fanciers. This is occurring worldwide, wherever bulbs grow wild and represent an enormous pressure towards extinction.

B. Where do the bulbs go?

Roughly two-thirds go to Holland. The other third to a range of countries, including the UK, the USA and West Germany. However, most of the bulbs entering Holland are subsequently re-exported worldwide, though indications are that the UK, USA and West Germany together take more than one-half of the wild bulbs trafficked through Holland. Since 1982 the Dutch share of the wild bulb marked has probably fallen back a little as increasing numbers of dealers from other importing countries deal directly with traders in the exporting countries.

C. How many bulbs and of which species?

The collection and trade in wild bulbs have been rising rapidly since World War II. By 1972, 25 million bulbs a year were being dug out of the ground in Turkey and exported. Ten years later the figure of 25 million had been exceeded for snowdrop bulbs alone. In Turkey, at least 20 types of bulbs have suffered exports in excess of 100,000 in one year. In each case these figures would be considered a minimum, as the number of bulbs exported from Turkey, without any documentation, can only be guessed. Elsewhere, Portugal, for instance, is exporting 1,000,000 wild *Narcissus* bulbs annually.

Export and import data have been grouped into genera. Details for individual species are extremely difficult, sometimes impossible to come by. Exports for most genera fluctuate considerable from year to year (within the overall upward trend) depending on weather, on the efforts of individual traders and collectors and to a lesser extent on fashions in importing countries. Consequently data for any specific year are of limited value.

Figures given below are '*A*' average values for exports from Turkey for the years 1983-1987 (the last year for which any accurate figures are yet available) inclusive and '*B*' (in brackets) the highest values for a single year, *since 1972*

		A	B
Anemone		6,642,000	(10,200,000)
Arum (inc. *Dracunculus*)	(Voodoo Lily, etc.)	115,000	(300,000)
Chionodoxa	(Glory of the Snow)	0	(58,000)
Colchicum	(Autumn Crocus, Meadow Saffron)	3,000	(50,000)
Cyclamen	(Cyclamen)	2,123,000	(5,000,000)
Eranthis	(Winter Aconite)	11,528,000	(13,510,000)
Fritillaria	(Crown Imperial, etc.)	406,000	(750,000)
Galanthus	(Snowdrop)	36,452,000	(40,000,000)
Geranium	(Geranium)	110,000	(240,000)
Gladiolus	(Gladiolus)	40,000	(202,000)
Iris	(Snake's Head Iris, etc.)	57,000	(207,000)
Leucojum	(Summer Snowflake)	8,318,000	(13,165,000)
Lilium	(Madonna Lily, etc.)	229,000	(595,000)
Merendera	(Merendera)	0	(2,000)
Muscari	(Grape Hyacinth)	1,000	(467,000)
Narcissus	(Narcissus)	26,000	(855,000)
Ornithogalum	(Star of Bethlehem, etc.)	11,000	(151,000)
Oxalis	(Oxalis, Wood Sorrel, etc.)	0	(20,000)

		A	B
Pancratium	(Peruvian Daffodil)	0	(10,000)
Scilla	(Squill, etc.)	60,000	(273,000)
Sternbergia	(Winter Daffodil)	292,000	(450,000)
Tulipa	(Tulips)	77,000	(265,000)
Urginea	(Sea Squill)	6,000	(20,000)

THE LAW

A. International

The legislation of the Convention on International Trade in Endangered Species of Wild Flora and Fauna ('CITES', now ratified by nearly 100 countries) is only relevant here at present to species of *Cyclamen*, all of which are on CITES-Appendix II, requiring that exports be monitored by means of the issuing of permits. Turkey has not yet ratified CITES. In November 1988 at the inaugural meeting of the CITES 'Plants Committee', at Kew Gardens, it was agreed to propose the addition of both *Galanthus* and *Sternbergia* to Appendix II of the Convention.

B. European Community

In implementing the CITES legislation regarding *Cyclamen*, all species have been granted the protection of listing Annex C2 of European Economic Community (EEC) regulation 3026/82. Three species have been given additional protection equivalent to being on Appendix I of CITES, thereby effectively banning their export, or the sale of wild collected specimens. These are *Cyclamen balearicum*, *C. graecum* and *C. creticum*. There is no general EEC legislation preventing the over-exploitation of threatened plant species.

C. National

The level of protection afforded to wild plant species varies considerably from country to country, as does the effectiveness of such legislation and its enforcement. Even a country, such as Turkey, which at first would appear to have a substantial package of relatively well-enforced legislation covering wild plants and their exploitation, suffers from subtle flaws in this legislation which render it largely useless. Under Turkish law a whole range of species are banned from export, with many more coming under a quota system with only a limited amount of 'wild' material being allowed out. 'Cultivated' material is not subject to restriction and it is in the interpretation of 'cultivation' that problems and massive loopholes arise.

DISEASE—THE HIDDEN THREAT

The implications of introducing unknown diseases with wild plants should not be ignored. Under UK legislation all plants (other than some consignments under 2Kgs.) have to be accompanied by plant health ('phytosanitary') certificates to be allowed into the country. The system is clearly not working. Dutch traders are allowed to issue their own plant health certificates for plants being re-exported. This is potentially a very dangerous situation. At best the insect pests and fugal spores that are often carried on wild bulbs ensure their rapid demise after planting. Under average garden conditions at least one-third of wild-collected *Cyclamen* and *Narcissus* planted in the UK will never appear above the soil. Few indeed will survive longer than one year. The contrast with the vigorous, healthy, artificially propagated plants

produced by Holland is enormous, yet at the end of the chain of trade the gardener is frequently given no indication whatsoever as to the foreign, wild origins of the plants he or she could be buying. At worst pests can spread to other plants in the garden, greenhouse or elsewhere, or even to horticultural and agricultural crops.

CONSERVATION IMPLICATIONS

The uncontrolled exploitation of any wild source is dangerous. Dozens of wild bulb species are under threat of over-exploitation. Exactly how close we are to extinctions of wild populations of whole species is difficult to assess. Some have already been lost. Recently, thousands of bulbs of the beautiful white-flowered *Sternbergia candida* were 'on the market' within two years of its discovery as a new species. It now seems uncertain whether any remain at its only confirmed locality. In Chile *Tecophilea cyanocrocus* has been completely wiped out in the wild by the bulb collectors. In 1981 a shipment estimated as containing a quarter of the then known population of the rare *Cyclamen mirabile* was confiscated by UK customs. They were labelled "*Cyclamen hederifolium*" as *C. mirabile* is banned from export from Turkey. Turkish *Cyclamen mirabile* are still on sale in the UK, now labelled as "*C. europeanum*" (a species which does not even occur in Turkey). In northern Spain a subspecies of *Narcissus* has been collected to extinction.

It is also important to note that hundreds of bulb species face substantial threats from other directions such as changes in agricultural practice and road and building developments. In combination with collectors these can be enough to push a species over the brink. Several *Narcissus* species imminently face this problem.

There are two sides to the trade. On the one hand the large volume trade in once widespread species with which this report is mostly concerned and, on the other, the specialists trade in the very rarest, choicest species of the interest to unscrupulous collectors and sometimes unwitting purchasers.

Little has yet been discovered about the supply to specialists collectors of the deliberately 'obtained' rarest species. The prosecution and conviction in 1987 of a UK-based trader for the illegal import of cyclamens and orchids has made suppliers wary of giving information about their sources. Nevertheless, all indications point to the fact that every year thousands of the world's rarest bulb species continue to be pulled out of their wild habitats merely to embellish the collections of specialist fanciers. Within the horticultural world this is truly an international scandal.

COLLECTION OR CULTIVATION?

The advantages of a cultivated plant over a wild-collected plant of the same species are legion. The cultivated plant is likely to be healthier, free from pests and diseases. The cultivated plant is easier to establish, having been raised in conditions broadly similar to those where it will finally grow. The cultivated plant does not have to suffer the abrupt break in growth that the wild plant does after uprooting. The cultivated plant can be expected to flower at a predictable time. The cultivated plant has been raised in conditions that need not be environmentally damaging. Furthermore, cultivation ensures a renewable, reliable supply of stock for trade.

Why then does collection from the wild continue? First, for countries where labor is cheap, the price differential is tipped in favor of wild plants. Second, the Dutch bulb trade has been importing bulbs for centuries and although the major part of their sales are home-produced plants, old habits die hard. Furthermore, there are those who simply have no concern for the future of wild species or at best mistakenly hold that their practices are not harmful.

However, in terms of the price differential, a few of the more forward-looking traders are beginning to realize the transient nature of this situation. From a purely commercial point of view, traders would be well advised to switch to controlled propagation before they find themselves having created a demand that cannot be supplied from dwindling wild resources. That the trade in wild collected plants can be severely harmful to natural populations is well established. Also, well established are the techniques that will be required to artificially propagate all those species that are being stripped from wild. The introduction of new species to cultivation is something for which the horticultural trade can be justifiably proud. The continued, unnecessary exploitation of wild populations of species that are easy to propagate in cultivation, is not.

The most exciting progress of all would be the establishment of artificial propagation in the countries of origin. Not only would this minimize environmental damage but would provide a secure, safe and reliable income where it is most needed.

Early attempts at such indigenous cultivation are in danger of badly misfiring. Some bulb species are now being 'cultivated' in the same countries from which they are being collected. However, this 'cultivation' does not fit into the usual understanding of the term, and does not take the pressure off the wild populations. What is happening is that wild collected bulbs too small to be accepted by Dutch buyers are being briefly transplanted for a year or two in fields near the exporters' warehouses until large enough for export. A few of these transplanted bulbs may naturally set seed or produce small offshoots during this time. Normally, however, partial or complete replenishment of these stocks is required every year with further deliveries of small wild collected bulbs. These transplanted wild bulbs are claimed as being artificially propagated. There is a further danger here, as if these procedures become widely established, it becomes economically logical for the traders to strip entire wild populations rather than only taking those plants judged to be of a saleable size at the time of collection. The transfer to cultivation of plants and seeds collected from the wild is one of the requirements of the birth of civilization, for it became obvious that propagation of one's own plants has significant advantages—not the least is increasing the volume and reliability of the 'crop', and avoiding the need to keep moving on as wild plant resources dwindled.

Millennia later, such important lessons have still not been fully understood. Plants are still being gathered from the wild in excessive quantities when now much advanced propagation techniques could produce better, healthier and ultimately cheaper plants, certainly at a fraction of the environmental cost.

RECOMMENDATIONS AND ADVICE

The Fauna and Flora Preservation Society, which funded much of the research on which this paper is based, are calling for action on a number of areas.

Legislation

A. Banning import of all wild collected species of bulbs —**except** where it has been clearly demonstrated that the levels of exploitation for the species concerned are indefinitely sustainable.
B. Instigation of legislation requiring labelling of horticultural bulbs' origins at the cost of sale and identification to species level on all transit, trade and health documents.
C. Strengthening the controls covering the issue of plant health certificates for re-exported plants, especially in Holland.

D. Addition of several genera (to include *Sternbergia* and *Galanthus*) to the Appendices of the Convention on International Trade in Endangered Species.

Advisory

E. Dissemination of advice to consumers on how to avoid buying bulbs removed from dwindling wild populations.

Research

F. Investigation of the 'undercover' trade in endangered bulb species

G. Assessment of the extent of artificial propagation of endangered bulb species **outside** their countries of origin.

N.B.—The research on which this paper is based was carried out by and on behalf of the Fauna and Flora Preservation Society, World Wildlife Fund (US) and the Wildlife Trade Monitoring Unit.

UPDATE ADDED IN PROOF

Since this paper was delivered there have been important changes relevant to the trade in wild-collected bulbs. In January 1990 the genera *Galanthus* and *Sternbergia* were placed alongside *Cyclamen* on Appendix II of CITES. International trade in any species of these genera requires the appropriate CITES licence. In May 1990, the Dutch Bulb Exporters Association reached an agreement with conservation groups to instruct its members to improve the labelling of exported bulbs. The phrase 'bulbs from wild source' is to be used for wild-collected bulbs by the end of 1990, and the phrase 'grown from cultivated stock' to be in place for artificially propagated bulbs by 1992. During 1989 and 1990, the Fauna and Flora Preservation Society has been developing its Indigenous Propagation Project which is designed to promote artificial propagation for export of threatened bulbous species on a small-scale, rural basis across three regions of Turkey. It is intended that this will not only reduce pressures on wild populations and provide local people with a much needed stable and safe income but also provide gardeners with higher quality bulbs. It is hoped that Indigenous Propagation Project activities will commence in 1990. In the UK many responsible traders are now committed to not stocking wild-collected plants.

The three most worrying aspects of the trade and those to which attention is now being turned are the specialist trade and collection of relatively small quantities of particularly rare, geographically restricted and highly-prized species, the collection from the wild *Narcissus* species and the 'opening up' of new geographical regions by those traders who persist in dealing in wild specimens, thereby not only damaging wild ecosystems and pushing some species to extinction but eroding the genetic base on which the trade itself ultimately depends.

CHILEAN MONOCOTYLEDONOUS GEOPHYTES TAXONOMIC CONSIDERATIONS AND THEIR STATE OF CONSERVATION

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INTRODUCTION

For many years I have been attracted by the beauty and diversity of the Chilean geophytic monocotyledons, observing them during numerous field trips, taking photographs, collecting herbarium material and seeds, even making every effort to grow them in my garden, but with very little success (Figure 1).

The Chilean territory is almost an ecological island, with geographical barriers isolating the biological communities from the rest of the continent and producing a high percentage of endemism.

Some 5200 species, arranged in 1035 genera and 200 families comprise the native flowering plants of Chilean flora, with 50% being endemic. Monocotyledons are present in 28 families, 220 genera and more than 1000 species. Between them, the petaloid geophytes are represented by some 180 species, with close to 90% of them endemic! They are found all over the country: in the vast deserts of the north, in the southern humid forests, in the Patagonian pampas, along the coast and in all mountains.

Several authors have studied this monocotyledonous group of plants over the last century, explaining the relationships between the species in different ways. As a consequence, many taxa have been created, and a number of classification have been proposed. Even today, specialists seem to disagree strongly among themselves and plants have changed taxa many times, especially those of the Superorder Liliiflorae. Also, the information about Chilean bulbs is very scattered throughout the botanical literature, making it very difficult to develop a coherent classification.

In 1981, Cronquist, in his "Integrated System of Flowering Plants", grouped all of them together in a single, big family, the Liliaceae. The same year, Dahlgren & Clifford published their "Comparative Study of the Monocotyledons", and some years later, "The Families of the Monocotyledons". There, through a comparative analysis of the morphology, anatomy, phytochemical characteristics, origin and evolution, present geographical distribution and other features regarding the natural species, they reached a very convincing organization of the group that works, as far as I am concerned, especially well for classifying the Chilean petaloid monocots.

CLASSIFICATION

SUPERORDER LILIFLORAE

Order	*Family*	*Subfamily*	*Tribe*	*Genus*
Asparagales	Amaryllidaceae		Hippeastreae	Rhodophiala
				Placea
				Traubia
			Stenomesseae	Famatina
				Stenomesson
				Phycella
	Alliaceae	Allioideae	Allieae	Ipheion
				Nothoscordum
				Tristagma
				Zoellnerallium
			Brodieae	Leucocoryne
				Pabellonia
				Triteleia
		Gilliesioideae		Ancrumia
				Erinna
				Garaventia
				Gethyum
				Gilliesia
				Miersia
				Solaria
				Speea
	Anthericaceae			Pasithea
				Trichopetalum
	Hyacinthaceae			Camassia
	Tecophilaceae			Conanthera
				Tecophilaea
				Zephyra
Liliales	Alstroemeriaceae			Alstroemeria
				Bomarea
				Leontochir
	Iridaceae		Tigrideae	Calydorea
				Herbertia
				Tigridia
			Sisyrinchioideae	Chamelum
				Sisyrinchium
				Libertia

Order	*Family*	*Subfamily*	*Tribe*	*Genus*
Liliales	Orchidaceae			Aa
				Bipinnula
				Brachystele
				Chloraea
				Codonorchis
				Gavilea
				Habenaria
Burmanniales	Corsiaceae			Arachnites

The present report, a preliminary one, has the aim of showing current knowledge about this group in Chile. The first part is a proposal for a new taxonomic organization for the genera in the taxa proposed by Dahlgren *et al*. Next is a list of species, distribution areas and conservation status.

It is true that more collecting and research is still needed, but we think that any information now, even if it is brief, is better than none, especially if it is relevant to rare or endangered plants.

Finally, a list of synonyms is presented.

Figure 1. The author in a field of *Rhodophiala* (All photos by H. Koopowitz)

SYSTEMATICS

Studying the Dahlgren books, we note that almost all of the Chilean petaloid monocots (except Bromeliaceae) are located in the Superorder Liliiflorae,i.e. in the orders Asparagales, Liliales and Burmanniales, with some 180 species, 40 genera and 9 families having geophytes: Amaryllidaceae, Alliaceae, Anthericaceae, Hyacinthaceae, Tecophilaceae, Alstroemeriaceae, Iridaceae, Orchidaceae and Corsiaceae. Liliaceae, traditionally included in the Chilean flora, does not have, according to this new classification, any representatives.

THE CHILEAN GEOPHYTE MONOCOT FAMILIES

Superorder Liliiflorae

A. Order Asparagales

1. AMARYLLIDACEAE (St. Hilaire 1805) brings together the genus *Placea*, *Rhodophiala* and *Traubia* in the tribe Hippeastreae, and *Famatina*, *Stenomesson* and *Phycella* in the tribe Stenomesseae, with a great number of described plants with pretty flowers, widely distributed all over Chile and in many other countries of South America.

2. ALLIACEAE (J.G. Agardh 1858) is easily divisible into two natural sub-families (Allioideae and Gilliesioideae), all the genera that were previously included in the Liliaceae. In the Allioideae there are 2 tribes. The first one, Allieae, contains *Ipheion*, *Nothoscordum*, *Tristagma*, and *Zoellnerallium*. The second one, Brodieae, includes *Leucocoryne*, *Pabellonia* and *Triteleia*. The sub-family Gilliesioideae includes a number of generally weak and inconspicuous plants, with typical flower characters. Nearly all are rare and poorly collected or grown, i.e. *Ancrumia*, *Erinna*, *Garaventia*, *Gethyum*, *Gilliesia*, *Miersia*, *Solaria* and *Speea*.

3. ANTHERICACEAE (J.G. Agardh 1858) encompasses the monotypic genus *Pasithea* and *Trichopetalum*.

4. HYACINTHACEAE (Batsch 1802) is the prefect family to include *Camassia*, with its racemose inflorescence, so different from the umbellate ones that distinguish the other species of the Order.

5. TECOPHILACEAE (Leybold 1862) is a family mainly circumscribed to the Southern Hemisphere with 6 genera: two in South Africa, one in California (*Odontospermum*), and three endemic to Chile: *Conanthera*, *Tecophilaea* and *Zephyra*, the latter with some 10 species of elegant blue or whitish flowers (Figure 2).

B. LILIALES is represented in Chile by three very broad families:

1. ALSTROEMERIACEAE (Demortier 1829) with *Alstroemeria*, *Bomarea* and *Leontochir*. *Alstroemeria* brings together some 50 species, 30 to 40 in Chile. They grow between Tocopilla (23° lat. S.) and Patagonia (55° lat. S.), and from the coast to the tree line up in the Andes. Bomarea in contrast, has some 150 species in the American tropics, but only 3 species in Chile, 2 of them really Peruvian (*B. engleriana* and *B. involucrosa*), with their southern distribution limit in the high cordillera of the Chilean First Region. *Leontochir* is a monotypic genus, with *L.ovallei*, a rare plant growing in a coast oasis of the Atacama desert.

2. IRIDACEAE (A. de Jussieu 1789) is represented by some 10 genera and 30 species. All of them are perennials, but only three genera have corms: *Calydorea*, *Herbertia* and *Tigridia*. It is worthwhile to mention here some Iridaceae provided with small rhizomes and beautiful flowers: *Sisyrinchium*, *Solenomelus*, *Chamelum* and *Libertia*.

3. ORCHIDACEAE (A. de Jussieu 1789) with 7 genera of terrestrial orchids (*Aa*, *Bipinnula*, *Brachystele*, *Chloraea*, *Codonorchis*, *Gavilea* and *Habenaria*) and some 50 species (not analyzed in this paper).

C. ORDER BURMANNIALES The Order includes only three families, one of which occurs in Chile.

1. CORSIACEAE (Beccari 1878), a monotypic family with *Arachnites uniflora*, a rare, pale brown plant, with big, unisexual, zygomorphic, spider-shaped flowers and leafless stems, and with a wide but discontinuous distribution in woody areas between Santiago and Magallanes.

The degree of adaptability of some of these plants to different environmental conditions is sometimes astonishing. For instance, in the Atacama, one of the driest deserts in the world, with a mean annual rainfall of 25mm, and where periods of completely rainless years are common, various bulbous species, in extensive and relatively dense populations occur, i.e. *Rhodophiala*, *Leucocoryne*, *Zephyra*, *Camassia*, *Alstroemeria*, etc. There, soil surface temperature can reach extremely high levels, but no data are available relative to the survival of seeds or seedlings.

THE SPECIES, AREAS OF DISTRIBUTION AND STATE OF CONSERVATION

From the 250,000 vascular plants existing throughout the planet, a great proportion are endangered and have some degree of conservation problems, including some 85,000 species in Latin America.

In Chile, many actions are being taken in order to know more about the dramatic loss of vegetation. It appears that the tendency of destruction is slowing down, and it seems to be less than in other countries of the area. Even so, inappropriate management of the environment, insufficient knowledge and poor ecological awareness, produce severe damage in a great number of biological communities.

Extinction of plants has been the subject of many recent publications. All authors agree that the major danger for natural ecosystems is centered in the growing demographic pressure and consequent over-use of natural resources.

Concerning the conservation status of Chilean geophyte monocots, very little has been done. In 1976, Ravenna published a paper on "Iridaceae, Amaryllidaceae and American Neotropics". Munoz Pizzaro, in 1971, edited his book, "Chile, Plants on Extinction", in which he analyzed some 70 species of endangered plants, including 10 of those that are of interest here. He described classical cases of total disappearance of beautiful flowers, like *Tecophilaea cyanocrocus*, one of the prettiest Chilean corms. This species was described in 1862 by Leybold, who emphasized the ornamental qualities of the plant. Hearing about this exotic beauty, horticulturists got so enthusiastic collecting it, that today, not one single Tecophilaea can be found in habitat.

Bulbous plants, Amaryllidaceae in particular, are a special group from the point of view of conservation. This is due to their distinctive features that make them particularly vulnerable. These characters, which derive from their biology and differ from the man-made problems, include long generation time, incompatibility factors, disease susceptibility and specialized cultural needs (Koopowitz, 1986).

Figure 2. *Zephyra elegans*

Figure 3. *Alstroemeria schizanthoides*

Figure 4. *Leucocoryne ixioides* and *Placea arzae*

Many botanical specialists in Chile think that all native plants in the country are vulnerable. Personally, I am not so pessimistic and still have confidence in a growing awareness of my countrymen. Even so, we have to be realistic. Many species, although abundant in habitat, are dangerously threatened by diverse anthropogenic menaces, such as the growth of agricultural and urban areas, overgrazing, erosion and man-made fires, all of which deeply disturb biological communities. Also important are direct effects on plant populations, such as the digging up of bulbs and cutting of flowers for commercial purposes, such as occurs with *Leucocoryne* spp., *Placea* spp., *Alstroemeria* spp. (Figure 3), *Pasithea caerulea*, *Phycella bicolor*, etc., that arrive by the millions at the flower markets of the cities.

The following is an effort to place the known Chilean species in the IUCN categories of conservation: Extinct (Ex), Endangered (E), Vulnerable (V), Rare (R), Out of Danger (O), Indeterminate (I), Insufficiently Known (I).

CONSERVATION STATUS SUMMARY

FAMILIES	NO. OF GENERA	NO.OF SPECIES	CONSERVATION STATUS					
			Ex	E	V	R	K	O
AMARYLLIDACEAE	5	41		1	8	12	17	3
ALLIACEAE	14	42	—	4	13	6	12	7
ANTHERICACEAE	2	2	—	—	—	—	—	2
HYACINTHACEAE	1	1	—	—	—	—	—	1
TECOPHILACEAE	3	11	1	—	2	2	2	4
ALSTROEMERIACEAE	3	35	—	1	15	9	3	7
IRIDACEAE	3	3	—	—	2	1	—	—
CORSIACEAE	1	1	—	—	—	1	—	—
TOTAL: 8	32	136	1	6	40	31	34	24

CONCLUSIONS

Concern and enthusiasm arise at the end of this analysis of the State of conservation of Chilean geophytic petaloid monocotyledons: Too many "Insufficiently Known" taxa appear; i.e. 34 in a total 136 analyzed plants.

It is, without any doubt, a difficult group, but also a fascinating one. It is a great challenge for the future to complete the missing data by collecting properly and systematically for herbaria, to learn more about the relationships between the taxa, their biology, ecology and conservation problems and, also, how to grow them properly.

In Chile, the study of the chemistry of native plants has begun, but we still do not know what important compounds bulbous plants might contain. Of the species mentioned, a couple are known to have reserve parts which are edible, such as "gnao" (*Conanthera* spp.), "liuto" (*Alstroemeria ligtu*) and the corms of *Tecophilaea cyanocrocus*. Would they be tasty? Maybe delicious, and perhaps this was another factor that drove the plant into extinction.

What is obvious is their potential as ornamentals. Many of them have been grown for decades in Europe and the United States, like the different varieties of *Alstroemeria*, *Placea*, *Rhodophiala*, *Leucocoryne*, etc. (Figure 4). Finally, I think of the beauty of *Zephyra elegans*, *Leontochir ovallei*, *Pasithea caerulea*, *Conanthera*, *Herbertia*, *Calydorea xyphioides* (Figure 5) or *Tigridia philippiana* as marvelous genetic material for the gardens of future.

I would like to thank my friends, Dr. Alan Meerow from the University of Florida and Mr. J. A. Castillo of Buenos Aires, a Director of the American Plant Life Society, for their wise observations and suggestions about this paper.

LITERATURE CITED

Bayer, E. 1987. Die Gattung Alstoermeria in Chile. **Mitt. Bot. Staat. Munich**.
Dahlgren, R., H. Clifford, Y P. Yeo 1985. The Families of the Monocotyledons. Springer-Verlag, Berlin.
Fuentes, F. 1921. Nota sobre los Notoscordios Chilenos. **Rev. Chil. Hist. Nat**. Santiago.
_____, 1929. Indice y comentario sobre las Liliáceas Chilenas. **Bol. Mus. Hist. Nat**. 105-126. Santiago.
Gay, C. 1853. Historia Física y Política de Chile. Tomo VI.
Hutchinson, J. 1939. The Tribe Gilliesieae of Amaryllidaceae. **Herbertia**
Koopowitz, H. 1986. Conservation Problems in the Amaryllidaceae. **Herbertia** 42:
International Union for Conservation of Nature and Natural Resources 1978. The IUCN Red Data Book. Kew, England.
Marticorena, C. & M. Quezada 1985. Catálogo de la Flora Vascular de Chile. **Gayana 42** (1 & 2)
Moldenke, H. 1959. Amaryllid Genera and Species. **Plant Life**
Munoz Pizarro, C. 1960. Las Especias de Plantas descritas por Philippi en el Siglo XIX. Edic. Univ. de Chile.
_____, 1966. Sinopsis de la Flora Chilena. Edic. Univ. de Chile.
_____, 1971. Chile: Plantas en Extinción. Edic. Univ. de Chile.
Reiche, K. 1893. Beitrage zur Kenntnis de Liliaceae: Gilliesieae. **Engler Bot. Jahrb**. 16:271.
Traub, H. 1963. The Genera of Amaryllidaceae. American Plant Life Society, La Jolla, California
_____, 1972. The Order Alliales. **Plant Life** 129-131.
Traub, H. P. & H. Moldenke. 1949. Amaryllidaceae: Tribe Amarylleae. American Plant Life Society, Salinas, California.
Traub, H. P. & J. Uphof 1939. Revision of *Amaryllis* I. **Herbertia** 5:114-131.
_____, 1939. Revision of *Amaryllis* II. **Herbertia** 6:146-154.

APPENDIX I

LIST OF SPECIES, DISTRIBUTION AREAS AND CONSERVATION STATUS.

SPECIES	DISTRIBUTION	CONSERVATION STATUS
AMARYLLIDACEAE		
PLACEA		
amoena	Dpt. Ovalle, Tulahuen	R
arzae	Santiago Mtns, Renca	V
davidii	Prov. Santiago, Maipo valley	R
germainii	Valparaiso Mtns, La Campana	R
RHODOPHIALA		
advena	Metropolitana and Vth Region	0
ananuca	Prov. Atacama (Caldera, Copiapo)	0
andicola	Antuco, Linares, Chillan Mtns	R
angustifolia	Santiago, Maipo Valley	K
araucana	Andes of Araucanía, Cupulhue	R
bagnoldii	South II to Ivth Regions	O
bakeri	Cordillera of Talca	R
berteroana	Rancagua	K
biflora	Valdivia, near San Jose	K
chilense	Southern sandy places	K
colona	Araucanía, from Renaico to Temuco	R
consobrina	Santiago Mtns	K
fulgens	Santiago Mtns	R
gayana=phycelloides?	Santiago Mtns	K
laeta	Antofagasta prov. coast	V
lineata	Metropolitana Region	E
moelleri	Araucanía	K
montana	Talca, Cordillera de San Francisco	K
ovalleana	Ovalle	K

SPECIES	DISTRIBUTION	CONSERVATION STATUS
AMARYLLIDACEAE		
RHODOPHIALA (continued)		
phycelloides	Andes of Chile	K
pratense=laeta	Atacama desert coast	V
purpurata	Prov. Linares Mtns	K
rhodolirion	San Fernando, Andes Mtns	K
roseum	Chiloe islands	K
solisii	Maule Region, Chillan	K
splendens	Prov. Curico	K
tenuiflora	Prov. Santiago, Valle Largo	K
tiltilensis	Prov. Santiago, Til-Til	R
uniflora	Cachinal de la Costa	K
PHYCELLA		
australis	Prov. Talca, Maule valley	V
bicolor	Coast and inland, Central zone	O
ignea	Mountains of Central zone	V
scarlatina	Prov. Coquimbo,Hurtado,Tulahuen	R
FAMATINA		
andina	Santiago Mtns, Loma del Viento	V
maulensis	Talca Mnts, Laguna del Maule	V
STENOMESSON		
chilense	I Region Mtns, 3000m	R
ALLIACEAE		
ALLIOIDEAE		
IPHEION		
sessile	Santiago Mtns, Las Arañas	R
NOTHOSCORDUM		
inodorum	Cosmopolitan	O
mahui		K
nublense	Ñuble to Valdivia,coast and inland	K
serenense	Prov. Coquimbo, Salala	V
striatellum		K
TRISTAGMA		
leichtlinii	Santiago Mtns	K
nivale	High Andes, Central provinces	O
ZOELLNERALLIUM		
andinum	30-35° lat. S, 2500-3500m	O
LEUCOCORYNE		
alliacea	Aconcagua to Araucania, 900-1300m	O
angustipetala	Prov. Coquimbo, inland, 1000-1500m	V
appendiculata	Iquique to Caldera,coast, 400-800m	V
conferta	Aconcagua and Coquimbo, 1000-1200m	R
coquimbensis	Coquimbo, Valparaiso, Aconcagua	V
ixioides	Central provinces	V
macropetala	Coquimbo and Atacama Provinces	V

SPECIES	DISTRIBUTION	CONSERVATION STATUS
ALLIACEAE		
LEUCOCORYNE (continued)		
odorata	Central provinces	V
pauciflora	Aconcagua, Valparaiso, Santiago	V
purpurea	Coquimbo Province coast	V
violacescens	Aconcagua and Santiago Provinces	V
PABELLONIA		
oxypetela	Coquimbo and Atacama inland plains	K
incrasata	Antofagasta and Atacama	O
TRITELEIA		
berteri	Valparaiso hills	O
bivalvis	Central Provinces	O
gaudichaudiana	Valparaiso hills	K
poeppigiana		K
porrifolia	Santiago Mtns	V
violacea	San Fernando Mtns	K
GILLIESIOIDEAE		
ANCRUMIA		
cuspidata	Coquimbo Region	E
ERINNA		
gilliesioides	Metropolitana Region, San Ramon	E
GARAVENTIA		
graminifolia	Metropolitana Region, Renca hills	E
GETHYUM		
atropurpureum	Metropolitana Region, Peñalolén	E
GILLIESIA		
curicana	Curicó Mtns, Las Tablas	R
gaudichaudiana		K
graminea	Aconcagua and Valparaiso Provinces	V
monophylla	Araucanìa	K
montana	Volcán Antuco	K
MIERSIA		
chilensis	Aconcagua to Maule	O
cornuta	IV Region, Cuesta El Melón	R
SOLARIA		
miersioides	Santiago, Valparaiso, Linares	K
SPEEA		
humilis	Santiago, Valparaiso	R
triloba	Prov. Santiago, Chicauma, 1700m	R
ANTHERICACEAE		
PASITHEA		
caerulea	Tocopilla to Valdivia	O
TRICHOPETALUM		
plumosum	Antofagasta to Central Provinces	O

SPECIES	DISTRIBUTION	CONSERVATION STATUS
HYACINTHACEAE		
CAMASSIA		
biflora	Antofagasta-Valparaiso, Argentina	O
TECOPHILACEAE		
CONANTHERA		
bifolia	Central Provinces	O
campanulata	Antofagasta and Central Provinces	O
minima	Bio-Bio Region, Mulchen	K
sabulosa	Coquimbo Region, sandy coast	V
simsii		K
tenella	Central Provinces, San Antonio	R
trimaculata	Central Provinces	V
urceolata	Prov. Huasco, coast	R
TECOPHILAEA		
cyanocrocus	Metropolitana Region	Ex
violaeflora	Coquimbo to Santiago	O
ZEPHYRA		
elegans	Iquique to Coquimbo, coast	O
ALSTROEMERIACEAE		
ALSTROEMERIA		
andina complex	26-31° lat. S, 2900-3700m	R
angustifolia complex	31-33° lat. S	O
aurea complex	36-42° lat. S, 200-1800m	O
crispata	29-30° lat. S, 1100-1300m	R
diluta complex	35° lat. S (Talca)	K
excerens	34-36° lat. S, 1500-2100m	K
garaventai	El Roble & Vizcacha Mtns, 2000m	V
graminea	25-27° lat. S, coast, 0-400m	V
hookeri	complex 35-37° lat. S, 0-300m	O
kingii	27-28° lat. S, 0-750m	V
leporina	29-30° lat. S, 900-2000m	V
ligtu complex	33-38° lat. S, 0-800m	O
magenta	31-32° lat. S, 0-700m	V
magnifica complex	29-33° lat. S, 0-200m	V
modesta	29-31° lat. S, 200-1500m	V
pallida	33-34° lat. S, 1500-2800m	O
patagonica	46-54° lat. S, 0-900m	V
paupercula (violacea)	22-27° lat. S, 0-200m	V
pelegrina	32-33° lat. S, 0-50m	V
philippi	28° lat. S, Carrizal Bajo, coast	R
polyphylla	28-29° lat. S, 0-800m	R
presliana complex	37-39° lat. S, 200-2000m	R
pseudospathulata	36° lat. S, 1000m	K
pulchra complex	32-38° lat. S, 0-1000m	V
revoluta	33-38° lat. S, 0-1800m	O
schizanthoides	30° lat. S, 800-1900m	V
spathulata	33-35° lat. S, 2000-3000m	V
umbellata	33-34° lat. S, 2000-3000m	V

SPECIES	DISTRIBUTION	CONSERVATION STATUS
ALSTROEMERIACEAE		
ALSTROEMERIA (continued)		
versicolor	34-35° lat. S, 250-1700m	R
werdermannii	28-29° lat. S, 0-50m	R
zoellnerii	33° lat. S, 1500-1800m	V
BOMAREA		
engleriana	Andes I Region, 3500-3700m, Peru	R
involucrosa	Dpt. Arica, 3500m, Peru	R
salsilla	Valparaiso to Valdivia	O
LEONTOCHIR		
ovallei	28° lat. S, Carrizal Bajo, coast	E
IRIDACEAE		
CALYDOREA		
xyphioides	Prov. Valparaiso hills	V
HERBERTIA		
lahue	Valparaiso-Valdivia(discontinuous)	V
TIGRIDIA		
philippiana	Atacama coast	R
CORSIACEAE		
ARACHNITES		
uniflora	Santiago to Magallanes	R

APPENDIX II

LIST OF THE CHILEAN SPECIES AND SYNONYMS

SUPERORDER LILIFLORAE

ORDER ASPARAGALES

AMARYLLIDACEAE J. St. Hilaire 1805.

HIPPEASTREAE

PLACEA Miers ex Lindl. 1826

amoena Phil.
arzae Phil.
davidii Rav.
germainii Phil.
grandiflora Lem.
lutea Phil.
ornata Miers ex Lindl.

RHODOPHIALA C. Presl (*Amaryllis* L. 1753; *Hippeastrum* Herb.1821; *Phycella* Lindl. 1825; *Rhodolirium* Phil.1857; *Habranthus* Baker 1878;

advena (Ker-Gawler)? (*Amaryllis* L. 1753; *Hippeastrum advenum*; *Habranthus pallidus*; *Habranthus miniatus*; *Habranthus hesperius*; (*Amaryllis valparadisiaca*; *Chlidanthus cummingii*; *Habranthus mendocinus*; *Myostemma advena*; *Eustephia macleanica*; *Hippeastrum pallidum*).

ananaca (Phil.)? (*Habranthus ananacus*: *Hippeastrum ananacum*).

andicola (Poepp.)? (*Amaryllis andicola*; *Habranthus andicolus*; *Hippeastrum andicolum*; *Zephyranthes andicola*).

RHODOPHIALA (continued)

angustifolia (Phil.) ? (*Amaryllis angustifolia*)

araucana (Phil.) (*Amaryllis araucana; Habranthus araucanus, Hippeastrum araucanum*).

bagnoldii (Herb.)Traub. (*Amaryllis bagnoldii; Habranthus bagnoldii; Habranthus punctatus; Hippeastrum bagnoldii; Hippeastrum punctatum*).

bakeri (Phil.) ? (*Amaryllis bakeri; Habranthus bakeri, Hippeastrum bakeri*).

berteroana (Phil.) ? (*Habranthus berteroanus; Hippeastrum berteroanum*).

chilense (L'Herit.) ? (*Amaryllis chilensis, A. chloroleuca; A. ochroleuca; Zephyranthes chloroleuca; Habranthus chilensis; Hippeastrum chilense*).

colonum (Phil.) ? (*Hippeastrum colonum; Habranthus colonum*).

consobrinum (Phil.) ? (*Amaryllis consobrina; A. consobriniana; Hippeastrum consobrinum, Habranthus consobrinum*).

fulgens (Hook. f.) ? (*Habranthus fulgens; Hippeastrum fulgens; Amaryllis fulgens*).

gayana (O. Kuntze) ? (*Hippeastrum gayanum; Amaryllis gayana*).

laeta Phil. (*Hippeastrum laetum*).

lineata Phil. (*Habranthus lineatus; Hippeastrum lineatum; Amaryllis lineata*).

moelleri (Phil.) ? (*Hippeastrum moelleri; Habranthus moelleri; Amaryllis moelleri*).

montana (Phil.) ? (*Hippeastrum montanum, Habranthus montanus*).

ovalleana Ravenna

phycelloides (Herb.)Hunz. (*Habranthus phycelloides; Hippeastrum phycelloides; Amaryllis phycelloides*).

pratense (Poepp.) ? (*Habranthus speciosus; H. pratensis; Rhodophiala amarylloides; R. volckmannii; Hippeastrum pratensis; Stephanoma elegans; Amaryllis pratensis*).

purpurata (Phil.) ? (*Hippeastrum purpuratum; Amaryllis purpurata; Rhodophiala andicola*).

rhodolirion (Phil.) ? (*Rhodolirion andinum; Hippeastrum andinum; Amaryllis rhodolirion*).

roseum (Sweet) ?

solisii (Phil.) ? (*Hippeastrum solisii; Habranthus flavus; H. solisii; Amaryllis solisii; A. flava*).

splendens (Renjifo) ? (*Habranthus splendens; Hippeastrum splendens, Amaryllis splendens*).

tiltilensis (Traub et Moldenke) ? (*Amaryllis tiltilensis*).

tenuiflora (Phil.) ? (*Hippeastrum tenuiflorum*).

uniflora Phil. (*Hippeastrum uniflorum*).

TRAUBIA Moldenke 1963. (Lapiedra, F. Phil. 1896)

modesta (Phil.)Rav. (*Rhodophiala modesta; Hippeastrum modestum; Lapiedra chilensis; Amaryllis modesta; Traubia chilensis*).

TRIBE STENOMESSEAE

FAMATINA Ravenna

andina (Phil.)Rav. (*Rhodophiala andina; Hippeastrum andinum*).

herbertiana (Lindl.)Rav. (*Phycella herbertiana; Hippeastrum herbertianum; Amaryllis herbertiana*).

maulensis Rav.

PHYCELLA Lindley 1824.

australis Rav.

bicolor Ruiz et Pavon (*Amaryllis cyrtanthoides; A. ignea; A. magnifica; A. demissa; Phycella crytanthoides; Ph. bicolor; Ph. brevituba; Ph. corusca; Ph. biflora; Ph. attenuata; Ph. magnifica; Ph. glauca; Ph. ignea; Ph. macraeana; Ph. obusifolia; Hippeastrum bicolor*).

scarlatina Rav.,

STENOMESSON Herbert 1821. (*Clinanthus* Herb.)

chilense Rav. (*S. humile* (Herb.)Baker ?).

ALLIACEAE J. G. Agardh 1858.
ALLIOIDEAE: ALLIEAE

IPHEION
sessile (Phil.)Traub. (*Triteleia sessilis* Phil.; *Tristagma sessile* Traub).

NOTHOSCORDUM Kunth 1842.
inodorum (Soland. ex Aiton)Nichols.
malui Traub.
nublense Rav.
serenense Rav.
striatellum (Lindl.)Kunth. (*Ornithogalum gramineum* Sims; *Nothoscordum gramineum* Kth.).

TRISTAGMA Poeppig 1833.
leichtlinii (Baker)Rav. (*Milla leichtlinii* Baker).
nivale Poeppig (*T. australe* Neger; *T. eremophila* Spegg.; *T. chubutense* Gand.).
subbiflora (Bert. et Colla)Rav. (*Allium subbiflorum* Bert.; *Nothoscordum subbiflorum* Bert.; *Brodiaea subbiflora*).

ZOELLNERALLIUM Crosa (*Nothoscordum* Kth.)
andinum (Poepp.)Crosa (*Ornithogalum andinum* Poepp.; *Allium? poeppigii* Kunth; *Nothoscordum strictum* Gay; *N. brevispathum* Phil.; *Nothoscordum andinum* (Poepp.)Fuentes).
ALLIOIDEAE: BRODIEAE

LEUCOCORYNE Lindl. (*Antheroceras* Bert. 1831; *Loucocoryne* Steud. 1841).
alliaceae Lindl. (*Brodiaea allioides; Leucocoryne montana; L. connivens; Antheroceras ornithogaloides*).
angustipetala Gay.
appendiculata Phil.
conferta Zoellner.
coquimbensis F. Phil.
ixioides (Hook.)Lindl. (*Brodiaea ixioides* Hook.; *Antheroceras odorum*).
macropetala Phil.
odorata Lindl. (*Leucocoryne foetida*).
pauciflora Phil.
purpurea Gay.
violacescens Phil.

PABELLONIA Quezada et Marticorena (*Chrysocoryne* Zoellner)
oxypetala (Phil.)Quez. et Martic. (*Leucocoryne oxypetala; Chrysocoryne oxypetala; Tristagma dimorphopetala* Gay; *Leucocoryne gayi; Leucocoryne dimorphopetala* (Gay)Rav.).
incrassata (Phil.)Quez. et Martic. (*Leucocoryne incrassata; Chrysocoryne incrassata; Stemmatium narcissoides* Phil.; *Leucocoryne narcissoides* Phil.).

TRITELEIA Douglas 1830
berteri Kunth (*Tristagma berteri*
bivalvis Lindl. (*Tristagma bivalve; Nothoscordum bivalve*).
gaudichaudiana Kunth
poeppigiana Gay
porrifolia Poepp. (*Brodiaea porrifolia*).
violacea Kunth

GILLIESIOIDEAE

ANCRUMIA Harvey
cuspidata Harv. ex Baker (*Solaria cuspidata*).

ERINNA Philippi
gilliesioides Phil.

GARAVENTIA Looser 1944. (*Steinmannia* F. Phil. 1884)
graminifolia (F. Phil.)Looser (*Steinmannia graminifolia* Phil.; *Tristagma graminifolia* (Phil.)Rav.; *Nothoscordum graminifolia* (Phil.)Traub).

GETHYUM Philippi 1873.
atropurpureum Phil. (*Solaria atropurpurea* (Phil.Rav.)

GILLIESIA Lindl.
curicana Rav.
chilense Lindl. ?
gaudichaudiana Kunth
graminea Lindl.
monophylla Reiche
montana P. et E.

MIERSIA Lindley
chilensis Lindl. (*Miersia myoides* Bertero)
cornuta Phil.

SOLARIA Philippi (*Symea* Baker 1871)
miersioides Phil.

SPEEA Loesner ex Krause (*Geanthus* Phil.)
humilis (Phil.)Loes. ex Krause (*Geanthus humilis* Phil.)
triloba Rav.

ANTHERICACEAE J. G. Agardh 1858.

PASITHEA Don. (*Anthericum* auct. non L.)
caerulea (R. et P.)D. Don (*Anthericum caeruleum* R. et P.; *Phalangium caeruleum* Pers.; *Cyanella illcu* Mol.; *Phalangium caeruleum* Mol.; *Stypandra caerulea* R. Br.).

TRICHOPETALUM Lindley (*Bottionea* Colla, *Bottinaea* Dahlgreen)
plumosum (R. et P.) (*Anthericum plumosum* R. et P.; *Bottionea thysanthoides* Colla; *Trichopetalum gracile* Lindl.).
stellatum Lindl. ?

HYACINTHACEAE Batsch 1802.

CAMASSIA Macbride (*Scilla* auct. non L.; *Fortunatia*)
biflora (R. et P.)Coc. (*Scilla triflora* Phil; *S. biflora* R. et P.; *S. geminiflora* (Herb.)Kunth; *S. chloroleuca* (Lindl.)Kunth; *S. argentinensis* Lillo; *Fortunatia biflora* (R. et P.)Macbride; *Ornithogalum chloroleucum* Lindl.; *O. geminiflorum* Herb.; *O. biflorum* (R. et P.)D.Don).

TECOPHILACEAE Leybold 1862.

CONANTHERA Ruiz et Pavon (*Cummingia* D. Don)
biflora R. et P.
campanulata (D. Don)Lindl. (*Cummingia campanulata* D. Don)
johowii Esp.
minima Grau
sabulosa Rav.
simsii Sweet
tenella (Sw. ex Kunth)Rav. (*Cummingia tenella* D. Don; *C. parvula* Phil.).

CONANTHERA (continued)
trimaculata (D. Don)Meigen (*Cummingia trimaculata* D. Don)
urceolata Rav.
variegata Fenzl

TECOPHILAEA Bertero ex Colla
cyanocrocus Leyb. (*Zephyra cyanocrocus* (Leyb.)Rav.)
violaeflora Bert. ex Colla (*Zephyra violiflora* (Bert. ex Colla)Rav.

ZEPHYRA D. Don
elegans D. Don (*Z. amoena* Dahlgreen).

LILIALES
ALSTROEMERIACEAE
ALSTROEMERIA L. 1762. (*Priopetalum* Grah. 1838; *Lilavia* Lehm. 1838; *Ligtu* L. 1863)
(Specific synonomy to be compiled by other workers)

Figure 5. *Calydorea xiphioides*

INTRODUCTION OF NEW BULBOUS CROPS IN THE NETHERLANDS

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INTRODUCTION

ALL over the world growers are showing interest in new crops. This interest requires knowledge about these new crops and about the way to collect material of these particular plants. More than 1000 genera are known of bulbous, cormous and tuberous plants all over the world.

Although much literature is available on these plants, only limited information can be found with respect to the potential value as cut flowers, pot plants, or garden plants. One aim of the new Bulbous crops project is to collect and arrange the relevant literature and to extract knowledge for the potential horticultural applications of these plants.

A second aim is to find ways to collect the interesting plant material, to study their characteristics under Dutch cultural conditions, and to advise the growers on growing, breeding and introduction of this new crops.

This project is approached as follows:

A. LITERATURE STUDY

Extensive literature surveys are performed on the genera of bulbous plants, to find out to which plant family they belong, to which genus they are related, how many species are known, what the natural habitat is, etc.

At the same these, if possible, answers might be found on questions about the flowering time, plant length, flower color, inflorescence, multiplication, etc.

On the basis of these data, some plants can be indicated with a provisional potential for horticultural use in the Netherlands.

At the moment about 500 genera, these data have been collected and stored in a computerized data bank.

An example of a date-chart is as follows:

Genus: *Cyrtanthus*
Family: Amaryllidaceae-Haemantheae
Synonym: *Anoiganthus*

A genus from about 50 species, bulb-shaped, probably not hardy. There are already some hybrids available.

Origin: South Africa
Related to : *Scadoxus, Haemanthus, Clivia, Vallota*
Color: Red, yellow, pink, white, orange
Plant length: 20-50cm
Flowering time: July-August
Inflorescence: More or less umbellate with 3-10 flowers

Multiplication: Offsets, seed, chipping or tissue culture may be possible.
Use: Cut flower, noteworthy is its a good keeping quality as a pot plant, garden plant?

Additional sources of literature data on these and related genera include:

Taxonomical descriptions of a genus or genera, monographs, descriptions of regional floras, research descriptions, multiplication methods, leaf and flower initiation, value for horticultural use, etc.

Although not present on the data-charts, such information will be arranged and stored in a data-bank.

B. To Find Ways to Obtain Material of Interesting Genera

All over the world contacts must be made with institutions and individuals that can be useful in this matter. Personal contacts appear to be very important.

Various important sources are:

— Botanical gardens; seed lists, collection lists and collections
— Research institutions/universities; research results, i.e. tissue culture, flower initiation, breeding, etc.
— Specialist growers; collections, shows, growing and breeding knowledge.
— Amateur growers collections, shows, growing and breeding knowledge.
— Collecting trips by yourself or others.

Again this information will be stored in a data base.

C. Collection of Materials

This is a second important phase in the introduction program. For a good prediction of the potential of a plant, it is very important that such a particular plant be in your own research program. That means, for instance, that research has to be performed in relation to multiplication, hardiness, storage problems, the purposes for use, etc.

At the moment we have a collection at from about 100 genera at Lisse.

The total collection consists of about 400 different plants (species, plant types or hybrids).

This collection came from Australia, Chile, Lesotho, Malawi, Colombia, United States and other parts of the world. From this plant collection an inventory is made including genus/species, family and place of collection, and growing conditions, flowering time, etc. under our condition in The Netherlands.

D. Participation and Collaboration of Growers and the Trade

Concurrent with the orientation research stage, the growers and trade can and must play an important role. The organization has been arranged in a manner that representatives form a kind of Accompaniment Committee. Such a committee also defines if a plant might have some prospects, and outlines what type of problems first have to be resolved. General interest can be generated by exhibiting plant material in shows, articles, meetings, lectures, etc.

It is very important that after initial culture experiments by the selected growers, a feedback response is necessary to define a research program for solving particular problems. In addition a good system must be developed for distributing plant material to the growers. If

growers and trade show interests increase in these special plant material may quickly be introduced into the market.

It is important to note that the choice of new plants or plant-types must be made by the growers and trade, since only they have the necessary knowledge of the growth and economic potential of a new crop. Introduced products can be intermediate products for breeding or selection purposes, but may also be a more or less final product. Also, when plant material is introduced, a good feed-back response is necessary to evaluate the results and the problems.

For an optimal feed back, meetings will be organized by the involved groups of people that have started with the new plant material, e.g. a group of people interested in the genus *Leucocoryne*). In addition The Bulb Research Center advises on problems and take part in the coordination of the research on these new products.

SUMMARY

— The Bulb Research Center, Lisse aids in the introduction of new bulbus crops by surveying of the literature to gather relevant information on bulbous, cormous and tuberous plants, and to collect and arrange the available knowledge on potential horticultural applications.
— Defining the characteristics of new crops for horticultural applications.
— Investigating ways to collect material and to make collections of material.
— Studying the collected material in field experiments and in other ways, to indicate the use for practical horticulture.
— Distributing material to growers and breeders, and to advise the growers and traders about multiplication, growing and breeding capacities of the promising new crops.

LITERATURE CITED

Koster, J. and A. J. Dop 1987. Nieuwe gewassen in de Nederlandse bolbloementeelt. **Vakablad voor de Bloemisterij** 15:32-35.

De Kleyn, E.H.J.M. 1984. Produktvernieuwing verlengt systematische verkleuring en afweging. **Vakblad voor de Bloemisterij** 25:39

Vonk-Noordergraaf C. 1984. Verzamelen van plantmateriaal draagt bij aan produktvernieuwing. **Vakblad voor de Bloemisterij** 25:30-31.

Lawson R.H. 1984. Search for success, new crops research in the USDA. **Florists Review** August 16, 1984 p. 38-41.

Kroon, G.H. 1988. Samenspel moet introductie nieuwe gewassen tot succes maken. **Vakblad voor de Bloemisterij** 24:58-59.1

A Review of Fifty Years of Commercial Lily Hybridizing in North America

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The enormous growth of the hybrid lily industry worldwide in the past twelve years from approximately 800 acres in 1977 to well over 6,000 acres in 1988 is due almost in its entirety to the early work of Jan de Graff and his associates at Oregon Bulb Farms in Sandy, Oregon. Their assembling together of a wealth of genetic material from a host of different sources laid the foundation for the commercial lily trade as it exists today. This paper is a tribute to those who were instrumental in bringing hybrid lilies to the exciting stage they are in today. It is also an appeal for others to continue their pioneering work, especially with the introduction of new species and hybrids into the breeding lines.

There are ninety species of *Lilium* scattered throughout the Northern Hemisphere and approximately twenty-two of these have been used to produce the hybrid lilies sold in today's market place. Some of these species have been used only recently and sparingly and much work has yet to be done to develop and perfect the hybrids. We must fully grasp how important it is to preserve the natural species. Many are already on endangered plant listings and every effort must be made to establish meaningful populations, both in their natural environment, and in cultivation. We can then do much to ensure that the unique beauty of both the species and hybrids from them endures for posterity.

The fifty years of experience gained in the hybridizing, selecting, testing and growing of hundreds of thousands of seedlings always underlined the necessity for clear rules and guidelines in a breeding program. These allow us to benefit from the lessons of the past and prevent us from repeating unfruitful lines. The following guidelines are compiled from the lessons learned from the years of experience:

1. A thorough knowledge of lilies, both species and hybrid, is essential if the work is to be meaningful.
2. A well-planned program needs to be outlined with expected goals clearly established. We can hybridize to produce outstanding clones and also uniform strains in species and certain hybrid populations.
3. Lilies selected from seedling populations must be of a color form and habit which will have high commercial appeal.
4. The varieties selected need to be strong growing. This "strength" applies both in clonal selection and in populations of seedlings from two given parents. The clones need to show strong natural multiplication and must also perform well from asexual propagation, both in scaling and tissue culture.
5. The tolerance to virus disease is critical for all clones increased for commercial growing. In the production of seedling strains, it is preferable that one parent at least is highly tolerant to virus. Commercial lilies need to persist and grow well despite infection; this quality is essential if lilies are to survive in gardens.

6. Lilies must have resistance to disease, especially basal rot which is caused by both Fusarium and Cylindrocarpum. A remarkable resistance to Botrytis blight has been found in some species and hybrids and this must be developed more fully.
7. The variety must be adaptable to commercial handling, storing and shipping. Bulbs that are less susceptible to bruising are preferred.
8. The varieties destined for cut flower and pot plant growing must be adaptable to year-round forcing. They need to grow satisfactorily under stress and especially in conditions of low light. The cut flower stems must store and ship well.

The clones need to be tested under field conditions for a preferable period of at least eight years. Disease susceptible varieties are naturally eliminated, strong clones emerge showing their rapid increase in volume and in the maintenance of strength and vigor.

Forcing trials are established for varieties judged to be promising for either cut flowers, or pot plants. These tests run concurrently with the field trials. A meaningful number of bulbs from each clone are vernalized and planted under forcing conditions the following winter, summer and fall.

We can now take a glimpse of what was accomplished in the past half century of commercial lily hybridizing. The first material used came from universities, research stations, small growers, hobbyists and plant collectors from all over the world.

Commercial lilies can be divided into three main groups—Asiatics, trumpets/Aurelians and Orientals. Asiatic Hybrids constitute over 90% of all lilies at present under cultivation worldwide.

ASIATIC HYBRIDS

Mid-Century Hybrids

This group of hybrids launched an industry and most were hybridized prior to the second World War. The species involved were *L. dauricum, L. wilsoni, L. davidii, L. tigrinum, L. bulbiferum* and *L. leichtlini*. Hosts of clones were selected originally and many succumbed to virus infection. Of the earlier selections, 'Enchantment', 'Harmony' and 'Tabasco' still survive.

Connecticut Hybrids

A group of hybridizers in New England working for unspotted Asiatic lilies used a spotless yellow form of *L.* ×*maculatum* called 'Helen Carol'. They produced a unique group of excellent hybrids. The species involved were in ways very similar to what were used to produce the Mid-Century Hybrids, except that the yellow forms of the species were chosen, i.e. *L. tigrinum* var. *flaviflorum* and *L. wilsoni* var. *flavum*. 'Connecticut King', 'Connecticut Beauty' (syn. 'Medallion'), 'Connecticut Lemonglow', and 'Sunray' are now widely grown commercially and are the most exceptional clones produced from these breeding lines.

Patterson Hybrids

The work of Prof. C.F. Patterson at the University of Saskatchewan in Saskatoon, Saskatchewan Canada, fifty years ago produced perhaps the most dramatic breakthrough in Asiatic lily hybridizing. Dr. Patterson made many crosses but by far the most significant was his cross between *L. davidii and L. cernuum. L. cernuum* carried the genes to produce a vast array of pastel colors, including pinks, peaches, wines, creams and whites. Dr. Patterson's clone, 'Edith Cecilia' was used to cross with a wide variety of upright and side-facing lilies. The second generation produced upright seedlings from clear pink to pure white. Exciting

results were obtained when these were crossed to the stronger clones from the Mid-Century Hybrids and related lines. The following clones from these crosses have weathered the storms of time—'Chinook', 'Challenger', 'Peachblush', 'Pirate', 'Gypsy' and 'Sterling Star'.

The work continued using strong clones from the Mid-Century Hybrids, Connecticut Hybrids, Patterson Hybrids and closely related lines. Many excellent clones have emerged—'Matchless', 'Melon Time' and 'Foxtrot' in orange; 'Goldmedal', 'Edith' and 'Impala' in yellows; 'Matador', 'Firecracker' and 'Firebrand' in reds; 'Alpenglow', 'Standby' and 'Zephyr' in pinks; 'Avalon', 'Colleen' and 'Snowcap' in whites; and 'Jetfire' and 'Duet' in bicolors. A series of genetically short lilies was developed from identical lines as the Mid-Century, Connecticut, Patterson and other closely related hybrids. This shortness was the result of inbreeding and the first was found by A. J. Porter of Parkside, Saskatchewan . He named this lily 'Red Carpet'. This work was continued to produce the "Pixie Series" which includes a wide range of colors.

A cross using virus-tolerant clones of two species *L. maximowiczii* var. *unicolor* and *L. dauricum* produced dramatic results; seedlings from the F_2 population producing unique and unusual colors and forms, including "Brushmarks." The best Brushmark seedling was crossed to 'Connecticut King' and this and succeeding generations produced unique and strong lilies. Named clones include 'Impact', 'Vanguard', 'Sundial' and 'Artistic'.

In more recent years, the strong and well-tested hybrids have been crossed with both related and unrelated species. *L. dauricum* crossed with the Mid-Century Hybrid 'Tabasco' and 'Connecticut King' produced seedlings with remarkable durability, uniformity and disease resistance. The populations were introduced as Rainbow and Sundrop Strains. Excellent clones selected from these strains included 'Aristo' and 'Sinai'. Another related species *L. wilsoni* var. *flavum* was crossed with 'Connecticut King' to produce several strong and virtually indestructible clones. These included 'Joanna' and 'Pollyanna', now grown in large numbers.

The work with unrelated species is, of course, a new adventure. Considerable success was achieved with *L. pumilum* used for its earliness, hardiness and fragrance, *L. lankongense* used mainly for its unique pink coloring and spicy fragrance and *L. concolor* for its tiny flowers, high bud count and early flowering.

L. longiflorum has, of course, been used as cut flowers and Easter lilies for many years. Colored lilies of this type have long been desired. Steps in this direction was achieved through embryo culture and some fertility was achieved in second generation crosses. Several Asiatic Hybrids in a variety of colors were used with clones of *L. longiflorum*.

The Chinese trumpet lilies have been very popular as garden plants for many years and only a few are grown as cut flowers. Their intense fragrance can be overpowering indoors. The work of Harold F. Comber, carried out just over thirty years ago, had tremendous significance and made hundreds of thousands of healthy bulbs of these lilies available in a wide spectrum of colors. Comber made hundreds of test crosses with the color groups over a period of years and produced F_1 strains which were remarkably true to color, form and flowering season.

The species involved in the ancestry of these lilies include *L. leucanthum* var. *centifolium* which is sold commercially as Black Dragon Strain and *L. regale*, which has been sold in considerable quantities since its introduction from China by Wilson in 1908. The other species used to produce these lilies are *L. sargentiae*, *L. sulphureum*, *L. myriophyllum* and *L. henryi*. The Sentinel and Green Magic Strains sold commercially involve L. regale, L. leucanthum and L. myriophyllum. L. sargentiae was the original source of color found in Pink Perfection Strain; other parents involved are not clear, but would include at least forms of *L. leucanthum*.

The other colors found in the trumpet and sunburst lilies is due to the influence of *L. henryi*. This Turk's-cap species was crossed with three different trumpet species by three separate hybridizers. *L.* ,×*aurelianense* produced by Debras was *L. sargentiae*×*L. henryi*; *L.* 'T. A. Havemeyer' produced by Tom Barry was *L. sulphureum*×*L. henryi* and *L.* 'White Henryi' produced by Leslie Woodriff was *L. henryi*×*L. leucanthum* var. *centifolium*.

The first two crosses produced most of the early material and, unfortunately, accurate records are unavailable of the earlier hybridizing.

The following strains evolved from the complex crosses between the trumpet species and L. henryi: 'Copper King', 'Golden Splendor', 'Moonlight', 'Golden Sunburst' and 'Heart's Desire'. Many fine clones have also been selected and upright and shorter trumpet forms are also available.

The Oriental lilies are the true aristocracts of the genus and any flower more beautiful is hard to imagine. The six parent species are all native to Japan with one exception, *L. speciosum* var. *rubrum* which is also found on mainland China and Taiwan.

All six species were eventually used at Oregon Bulb Farm and we can trace the history as the species were introduced into the breeding lines.

L. speciosum and *L. auratum* were first crossed in 1869 to produce *L.* ×*parkmannii*. This material was lost to virus infection. The work in the early part of this century was done in New Zealand by Dr. Yeates, Mr. Jury and Mr. Tuffery. The material from these gentlemen was brought together with similar hybrids and superior forms of both species from Dr. Emsweller and Dr. Slate in the United States, and also from Mr. Wada in Japan. Thus the foundation was laid for the early work with the Oriental lilies at Oregon Bulb Farms. The true breeding strains were preferred because of our ability to produce large quantities of disease-free material from seed. The following strains were introduced from the Speciosum×Auratum lines: 'Imperial Crimson', 'Imperial Silver', 'Imperial Gold', 'Jamboree' and 'Everest'. Excellent strains of both species were also produced. A great number of clones have been selected over the years and most commercially successful have been 'Cover Girl', 'Red Baron', 'American Eagle' and 'Journey's End'. Genetic dwarfs have also been developed, and were introduced as Little Rascals.

The delicate pink Japanese species *L. japonicum* was crossed with *L. auratum* by Dr. Norma Pfeiffer at the Boyce Thompson Institute and material sent to Oregon Bulb Farms. This cross introduced the earlier flowering habit, and also the clear pink coloring. The 'Imperial Pink', 'Pink Glory' and 'Celebrity' strains were introduced by combining the *L. japonicum*×*L. auratum* Hybrids with those from *L. speciosum* and *L. auratum* ancestry.

The clear pink *L. rubellum* is a very early species from higher elevations. The species was used by Norma Pfeiffer and Leslie Woodriff in earlier years and later by Oregon Bulb Farms. The strain 'Magic Pink' was *L. auratum* var. *platyphyllum*×*L. rubellum*. It was Leslie Woodriff who continued to cross the *L. rubellum* Hybrids with other Orientals and many clones were selected. Such clones as 'Fellowship', Rosario' and 'Le Reve' have proved to be the strongest. Much work still needs to be done before even finer hybrids from *L. rubellum* emerge.

The final two species *L. alexandrae* and *L. nobilissimum* have been used only sparingly, but dramatic results can be achieved in both cases. Both species were crossed with clones of *L. speciosum* to produce beautiful hybrids. *L. nobilissimum* was also crossed with 'Pink Glory' and 'Imperial Silver' strains to produce several clones of breath-taking beauty. These clones included 'Copellia', 'Sylvia', 'Swansong' and 'Giselle'.

The hybridizing of the past fifty years has indeed accomplished much, it has, however, simply opened a door to vast horizons of beauty yet to be explored.

SCHIZOSTYLIS—CULTIVATION AND BIOLOGY

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INTRODUCTION

SCHIZOSTYLIS is an iridaceous genus of probably only one species endemic to the mountains of South Africa. Its natural range includes southern Rhodesia, Transvaal and Swaziland southwest through Orange Free State, Natal, Lesotho, Transkei and the eastern Cape Province, especially in the Drakensberg Mountains. It is becoming rare in nature, at least in a part of its range, but is widely cultivated in cool-temperature climates. It is a rhizomatous, cormous perennial, usually found along streams or on rocks in the middle of streams, where the roots are continuously moist, but the leaves are in full sun.

The genus and type species, *Schizostylis coccinea*, with bright red flowers, was named by Backhouse and Harvey in the **Botanical Magazine** in 1864. A second, dubious species, *S. pauciflora*, was named by Klatt in **Linnaea** in 1867. This name is applied to material with pale pink flowers, but it is now generally considered to be merely a small, pink form of the more widespread and variable *S. coccinea*. *Schizostylis* has received a number of common names, the most generally accepted being kaffir lily. Others include crimson flag, flame lily, river lily, winter ixia, and a more recent name coined by one bulb supplier, autumn plumes.

CULTIVATION

The genus was brought into cultivation soon after its discovery and it remains popular in gardens in the northern hemisphere, especially the British Isles and the moderate Pacific Northwest coast of North America, as well as in New Zealand and cooler parts of Australia. It is now naturalized in southwestern England, western Scotland, Ireland and New Zealand.

The popularity of *Schizostylis* in cultivation is due to the late summer through-fall flowering habits. Moist soil and full sun to light shade are important for success in the garden. Under these conditions, the plants quickly spread underground, forming large clumps. Dry, poor soil, dry winds and high humidity on hot days are detrimental to the plants. In hotter climates they must be grown in partial shade and even then are not at their best.

MORPHOLOGY

The underground structures of *Schizostylis* consist of a small swollen corm at the base of the stem. Several fleshy rhizomes are produced at the base of the corm. These spread horizontally a few centimeters below the surface of the ground. The rhizomes are white at first, becoming brown and slightly wooly-fibrous as they mature. A few thick vertical roots are produced from the base of the corm and rhizomes. Rhizome growth may reach 10-15cm each year, resulting in rapid colonization under good growing conditions.

Bright green, slightly sickle-shaped leaves, 20-30cm long and approximately 1cm wide, are produced in sterile "rosettes" the first year. (In Vancouver the basal leaves are completely herbaceous in cold winters or partially evergreen. In slightly warmer climates, with milder winters, as in central and southern California, the leaves may remain completely evergreen).

In successive years the stronger rosettes send up flowering stalks, with strongly basally disposed leaves and a few reduced leaves upward. Flower stalk elongation begins in mid to late summer although it does not seem to be strongly controlled by temperature or day-length, as a few flower stalks may be produced at any time of the year. The stalks reach 35-50cm tall by flowering time in late summer or autumn.

Four to ten flowers are usually produced on each stem, with one or two open at once, each of these lasting up to four or five days. The inferior ovary and base of the curved, slender flower tube is concealed by overlapping green bracts at their bases. Tepals are usually identical, although the inner petals may be slightly broader than the outer sepals. The tepals are uniformly colored, red or pink throughout. Flowers tend to stay partially closed and globular on cool, cloudy days, but they open to a flat saucer-shape in full sun. The outward-facing open flowers are 3-5cm across. Typical of the Iridaceae, there are three stamens and distinctive to the genus are the three long styles split to the base of the mouth of the tepals. Slightly three-angled seed capsules mature quickly and become papery and open releasing 50-70 straw-colored, angular seeds.

PROPAGATION

Seeds may be germinated in a well-drained, sandy peat or loam soon after release from the capsules, without any stratification. A high percentage of the seeds usually germinate within a month. The seedlings are delicate and grass-like for their first few weeks and are subject to damping-off. Once pricked-out and established in flats or individually in small pots and the seedlings usually become vigorous and grow quickly. If started in a greenhouse in autumn or early winter the seedlings will often be large enough for some of them to flower in 6-8 months. They should all flower by the second year.

Propagation is usually done vegetatively, especially for cultivars, by digging and dividing established clumps, usually in spring and replanting the most vigorous rhizomes and rosettes. This should be done at least every third year, or the clump will become so crowded that only weak basal leaves and fewer flower stalks will be produced.

CULTIVARS

In addition to the common bright red wild form and the less-common wild pink forms, two cultivars have been grown for decades, plus a few newer ones, mostly of English garden origin. As is so often the case, there is much confusion in the names of the cultivars. Some so-called named cultivars are sold as seedlings and, of course, do not come true from seed. It is not uncommon for named cultivars sold by nurseries to turn out to be something other than what was promised. There is also confusion of names and descriptions in some of the general gardening books that mention cultivars.

The oldest cultivar of *Schizostylis* is 'Mrs. Hegarty', a medium rosy-pink found among a clump of wild red form in Count Galway, Ireland at the turn of the century and named in 1921. It and the next cultivar are the most generally available and widely grown of the cultivars. 'Viscountess Bing' is a later, paler pink form usually flowering into November or even December in mild years. 'Major' (also known as 'Gigantea') is similar to the typical wild red forms, but the flowers are larger and brighter red. Plants sold as 'Major' are often the wild form. 'Salmon Charm' is a sport of 'Major' with dusky red-pink flowers and one of the least attractive of cultivars. 'November Cheer', another sport of 'Major', or even more likely a hybrid with one of the pink cultivars, is the shortest and latest flowering cultivar. The flowers are pale pink, produced on stems about 15cm tall. The height is a desirable charac-

teristic as a garden plant, but flowering begins so late that in cooler climates the flowers often open just as cold rains or frosts arrive, spoiling the flowers. However, it is a good plant to use in hybridization because of its short, stiff stature. Four other relatively new cultivars are not as yet widely cultivated. 'Tambra' was named in 1970 from plants collected in the wild in Rhodesia, in the northern part of the range of the species. Its flowers are rose-pink and it begins to open in August, the earliest of all cultivars. Someone should save pollen and try crossing it with 'November Cheer'. 'Sunrise' with large pink flowers, 'Professor Barnard', deep husky pink and 'Rosalie' also pink, complete the quartet. There are a few other cultivar names listed in catalogs, but, based on the descriptions, some of these may be re-names of other cultivars.

White-flowered forms were unknown in *Schizostylis* until very recently. There are no named white cultivars as yet, but white individuals have been found in the wild very rarely. White ones are being grown in New Zealand, the United States and Canada, at least. The white form that the UBC Botanical Garden has grown from seed received from New Zealand is pure white, but the plants are tall and straggly and the tepals are slender. It is being crossed with pale pink forms in an effort to get a more desirable white form of better substance on sturdy plants.

Schizostylis has some potential as a cut flower, but so far it has been done on a very small scale. The flowers keep well as a cut flower, although the individual flowers do not always open fully indoors. It has been suggested that keeping them in a cool place overnight and then bringing them into a warm, bright room will cause the flowers to open fully.

BREEDING SPOTLESS *ALSTROEMERIA* IN JAPAN

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INTRODUCTION

BREEDING is a difficult task, often with unsuccessful attempts to reach a targeted goal. On the other hand, breeding work, especially for ornamental flowers, occasionally brings the unexpected pleasure of a great success.

It has been fortunate that three such successful experiences have occurred in my breeding program in *Alstroemeria*. The first was the selection in 1977 of the pink flower strain with ideal flower shape, which became an excellent parent of crosses in my breeding program. The second success was selection in 1979 of a single plant with spotless flowers from the progenies of crosses between the above mentioned parent and others, followed by repeated self pollination. This was an important event in the development of my breeding program in *Alstroemeria*, especially for the establishment of spotless strains. The third success was the selection in 1984 of a spotless red strain from which a group of spotless strains was developed.

Probably the most important event was the second success, the selection of a strain with spotless flowers, because this characteristic may have changed the consumer's concepts of alstroemeria flowers, at least in Japan. For this reason, this spotless selection may be considered as the premier event in my breeding program.

In this article, the breeding process of spotless strains of *Alstroemeria* will be described in some detail in relation with the changes that occurred in flower production and consumption of *Alstroemeria* in Japan.

CHARACTERISTICS OF FLOWER PRODUCTION AND CONSUMPTION OF *ALSTROEMERIA* IN JAPAN

Alstroemeria is considered to have been introduced into Japan in the latter part of the 19th century. It was marketed as a cut flower as early as 1930, but has not been become popular until recently, when housing and life-styles have been westernized in Japan. Corresponding to this recent trend toward westernized housing and life-style, western-style flower arrangements have been introduced and have become popular in Japan. It is natural that consumption of spray type flowers such as *Alstroemeria* has dramatically increased.

Parallel to this westernization, the production of cut-flowers of *A. ligtu* hybrids, initiated in 1975, was followed by the introduction of patented Dutch cultivars and dramatic increase in production around 1980. Thus, in a relatively short period of time, *Alstroemeria* became one of the most important cut-flowers in the Japanese market.

It should be mentioned that Japanese people have a special preference for certain types of ornamental flowers. They prefer simple and clear type flowers, while the flowers with spots, stripes or particular patterns have less market value. Therefore, one of the main goals in flower breeding is the elimination of those undesirable characteristics. For example, breeders have made extensive and intensive attempts in eliminating those undesirable characteristics in *Lilium maculatum* and in orchids, *Odontoglossum*, but with great difficulties.

Figure 1. Spotless white Miyake strain of *Alstroemeria*

Figure 2. Spotless peach-pink Miyake strain of *Alstroemeria*

Figure 3. Spotless red Miyake strain of *Alstroemeria*

Figure 4. Spotless yellow Miyake strain of *Alstroemeria*

In case of *Alstroemeria*, the unique pattern with spots and stripes in the flower is an attractive trait in most places in the world, while the same trait has been considered as a negative feature, especially in Japan. In most of my earlier breeding programs, all seedlings raised from crosses and self pollination showed spots and/or stripes. However, a plant without spots/stripes appeared spontaneously in one of the seedling populations. This was a most important event in this *Alstroemeria* breeding program.

Development and Establishment of Miyake Spotless Strains of *Alstroemeria*

Following are some details on the process for breeding spotless strains of *Alstroemeria*. The first *Alstroemeria* was detected among the seedlings of *Eremurus*, because the plant was different from the rest of the *Eremurus* plants. This unknown plant later produced pink-colored flowers with unique beauty.

The value of this new plant as a cut-flower was immediately recognized. First an attempt was made to increase the plants by growing as many seedlings as possible for marketing. After the nature of this plant became familiar the potential of possible improvement of this unique flower by breeding was realized.

Even though the name and origin of this *Alstroemeria* was not known, cross breeding was initiated by using Dr. Salter's hybrid and *A. ligtu* hybrids as parents. Plants with attractive flowers were not found in the early generations. However, as generations progressed, various types of new flowers segregated; large-flowered plants with clear-colored and round petals, plants with well reflexed (opened) flower petals, one with shorter pedicels, and compact-flowered inflorescences (umbrella-type) that are similar to *Nerine*.

The first fortunate event occurred at the time when the pink-flowered plant was found which was an excellent parent for the cross-breeding program because it had an outstanding flower color and shape. Moreover, the majority of plants in the selfed progenies also showed combinations of various highly desirable traits such as clear and crispy colors, well-opened petals, and short compact-type pedicels. These characteristics were superior to previous standards of *Alstroemeria* flowers. Some registered cultivars such as 'Miyake Magenta' and 'Miyake Opal' were selected from those plants.

With these breeding programs, it was possible to establish special strains—Miyake strains. These strains were used for numerous crosses with other strains such as Dr. Salter's hybrids, *A. ligtu* hybrids and others for further improvement. Numerous crossings and selfings were continued, and resulted in more than 10,000 plants grown for observation and selection. The single spotless plant was found among this vast number of plants; this was the second fortunate event in 1979 in this program.

The simple and fresh appearance of the new spotless flower was so impressive that I wanted to establish the spotless type flower in different color backgrounds. Many crosses were made between the original spotless and different colored plants. However, it was not successful in selecting the spotless type in different colors in the beginning; all plants in the first and second hybrid generations showed spotted/striped type flowers. At this point there seemed to be little hope for selecting spotless flowers in different colors. However, in the 3rd and 4th generations, various plants segregated spotless flowers of different colors, such as orange, apricot, and soft-pink. This result encouraged and stimulated me to continue further crosses, self pollination and selections. Every year tens of thousand of flowers were observed for the selection of better and more desirable plants. This selection work was a time-consuming but enjoyable task.

The third fortunate event occurred in 1984 when a unique plant with red-colored spotless flowers (Figure 3) was found that played an important role in widening the range of spotless type varieties. In the selfed progenies of this new spotless plant, more new spotless type plants with different colors were found which had never been seen before. These were so different from most of parents used for crossings, that it was totally unexpected and surprising. With this success in establishing various types of spotless strains in *Alstroemeria*, the goal of *Alstroemeria* breeding was almost accomplished. However, there was one missing color among the spotless strains, that was the pure white!

A concentrated effort of crossing and selection was initiated in 1982 to eliminate spots and stripes from the white flower.

The plants in the F_1 hybrid generation from the cross between "spotless pink" and spotted pure white showed a wide range of segregation on the color from dark pink to light pink to pure white. However, all white flowers had spots. From this F_1, a light pink spotless and spotted pure white were selected and crossed. Crosses were repeated with the same or similar combinations in the 2nd and 3rd generations but no spotless pure white flowers were found. Meanwhile, as generations progressed, plants with spotless flowers of very light pink color segregated. These very light spotless pink plants were repeatedly crossed with spotted white. The total number of plants grown for selection from these crosses may have been more than 100,000.

Finally, a plant with spotless pure white flowers was found and selected, as shown in Figure 1.

With the selection of the spotless pure white *Alstroemeria*, the primary goal in *Alstroemeria* breeding was reached after 14 years of hard but enjoyable work. Now there are spotless strains with various colors such as pure white (Figure 1), peach-pink (Figure 2), several pastel colored flowers which are delicate combinations of those primary colors.

It was relatively easy to select spotless strains with a wide range of different colors in 2 to 3 generations by crossing the original spotless pink with spotted lines of different colors, with the exception of spotless pure white. It was a difficult task to select a spotless pure white *Alstroemeria*.

Future Prospects in *Alstroemeria* Breeding

In spite of the success in developing a wide range of varieties with different flower shape and color, including various spotless strains, there are still some problems in breeding *Alstroemeria*.

One of the problems is the flowering habit. Most *Alstroemeria* plants bloom in the spring. If the varieties have strong marketability because of highly desirable traits, the expected increase in *Alstroemeria* production may have a negative effect on market price because of the possible disturbance in the supply-demand balance. Another problem which is related to this flowering habit may be unequal distribution of labor (man power) arrangements.

In order to expand the marketing period for *Alstroemeria*, various methods already have been and are being introduced into flower production practices, such as acceleration or suppression of flowering by cold storage of the rhizomes and/or culturing under controlled day-length. In addition to those methods of environmental control, it is also desirable to introduce new genetic elements for various flowering habits into the present cultivars. *Alstroemeria caryophyllaea* is a Brazilian wild species which carries desirable genetic traits such as evergreen growth and autumn-winter flowering habit. Foster (1948) has successfully developed various year-round flowering varieties by crossing *A. caryophyllaea* with *A. inodora*, *A. psit-*

tacina, and *A. nemorosa*. Similar attempts are being made to cross these species at Miyake Farm.

Another goal in *Alstroemeria* breeding is the development of varieties for use as potted plants. For this purpose, crosses are being made between *A. caryophyllaea* and *A. inodora*, *A. psittacina* and *A. pulchella*, and also other species with the expectation of developing dwarf or semi-dwarf *Alstroemeria*. Some of these species have traits such as better flower development and rather short plant height (40-50cm for pot culture) which is important for potted plants.

Many F_1 hybrids from those crosses are currently flowering. However, their characteristics are not completely satisfactory for the development of potted plants because of rather larger plant size, although they have a prolonged flowering period. We are still hoping for the possible development of potted-style plants among the progenies of some back crosses of these F_1's with parental species.

Still another goal in *Alstroemeria* breeding is the establishment of seed-type (annual) varieties. We have several genetically stable spotless strains that breed true (no segregation) in selfed progenies. Some of these grow vigorously and produce marketable cut flowers in the first seeding generation. Some of these will be officially registered as (annual) seed-type *Alstroemeria*. If this type of seed-propagated *Alstroemeria* is established, it will be economically valuable for growers.

In addition to those traits to be introduced and established in the cultivars as discussed above, there are other traits that are worthy of mention. Those are fragrance, double-petaled flower, and variegated leaf. *A. caryophyllaea* has a fragrance similar to carnation. However, when it is crossed with other species, the fragrance is not expressed in the F_1 hybrid, indicating its genetically recessive nature.

Finally, *Bomarea*, *Leontochir* and some other genera are related to *Alstroemeria*. These materials now are being used for intergeneric hybridization with *Alstroemeria* to develop new flowers. Attempts were made to cross these materials with *Alstroemeria* and some hybrid seeds were obtained, although the success rate was very low. Introduction of embryo-rescue techniques may enhance our success in producing these intergeneric hybrids.

It is my hope that this presentation has shown the fascinating features and wide-open possibilities for future improvement and development of more attractive new varieties in *Alstroemeria*.

I joined the American Plant Life Society because of the recommendation of the late Dr. Shuichi Hirao, who guided and encouraged me to engage in floricultural activities with a wide international view. On this occasion I would like to express my deepest respect and appreciation to the late Dr. Shuichi Hirao, and I dedicate this paper to him.

Thanks are extended to Professor Takumi Tsuchiya, Colorado State University, because of his encouragement for me to participate in this symposium and for his assistance in the preparation of this paper.

LITERATURE CITED

Adachi, Toko, M. Kamo and I. Miyake 1988. Discussion on the late Dr. S. Hirao's view on the "New Flower". **Garden Life** 9:6-9.

Foster, M.B. 1948. Fragrant Alstroemerias in Florida. **Herbertia** 15:78-79.

Hirao, S. 1983. *Alstroemeria*: Miyake strain (white) bred by Isamu Miyake. **Jour. Jap. Hort. Soc.** 83:15.

Miyake, I. 1981. Breeding *Alstroemeria*. **Garden Life** 9:52-53, 60-61.

_____1983. *Alstroemeria*—A rapidly raised new flower. **Jour. Jap. Hort. Soc.** 84:16-17.

_____1984. New varieties of Alstroemeria. **Agronomy and Horticulture**. No. 4:182-183.

_____1987a. Breeding *Alstroemeria*. **Shin-Kaki** (New Flower). 136:31-35.

_____1987b. Future prospect of seed propagating *Alstroemeria*. **Agronomy and Horticulture**. No. 6:135.

_____1988. A new face in the cut flower, *Alstroemeria*. **Ikebana Sogetsu** 180:48

Yukawa, T. 1988. Isamu Miyake's View on New Flowers. **Garden Life**. 8:6-9.

RESEARCH PROGRAM ON *HIPPEASTRUM*

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THE research program on *Hippeastrum* started a few years ago when a post-Doctoral candidate, Julie Dutilh, was interested in studying the Brazilian native species. She is here today at this Symposium. She will present her studies mainly on cytotaxonomy of this species, which she developed at the Cytology Department of the Instituto Agronomico.

Initially, focusing on the *Hippeastrum* research program, a collection of *Hippeastrum* was made, adding the efforts of Julie Dutilh and Luiz Matthes, who is Head of the Flower and Ornamental Plants Department.

BREEDING PROGRAM

Actually this collection has more than 150 different types. They are, in great majority, Brazilian native species, some of them collected in culture in home gardens, and also a group of old Dutch hybrids, which were without their original names. Almost all of those hybrids came from a private firm, Roselândia Agricola, Ltda.

Several crosses were done in the 1983 season, during the months of August to November. Although initially the objective of the program was a cytotaxonomy study, the crosses were specially done between species. But thinking on the possibility of a breeding program, several crosses utilizing Dutch hybrids were also done.

The seeds were sowed in a greenhouse, as soon as the pods were dried. The germination was good, but not all the crosses produced offspring. A few plants flowered after a year and half of sowing, but only in 1986 were the first observations on these hybrids made, and also those crosses aiming to get the second generation (self-pollination, sib and crosses between offspring).

In 1986 I started to work at the Flower and Ornamental Plants Department, and I was charged with pursuing the development of this program.

The list of the first crosses realized in 1983 is shown in Table 1.

In the second generation it was noticed the sib crosses produced very bad results. The best results were obtained by crossing different offspring by accident (Table 2).

In the following year, 1987, the greenhouse was taken over by another department and the plants were transferred to a field at São Roque Experimental Station. During this there was no observation of the hybrids nor were crosses made.

It was noticed that some lines showed problems on adaptation to the new climate and soil conditions. Their vegetative development was poor, and some plants were lost.

In field conditions a virus infected almost all of plants, while in the greenhouse only half of the plants had shown symptoms clearly. After this the hope of identification of virus-resistant plants practically disappeared.

We were able to evaluate the qualities of the hybrids during the season of 1988. A filing card system was established where we recorded the following characteristics (Figure 1).

During this season we made 104 successful crosses, which are germinating at this time.

Actually the objective of the program is the creation of new varieties with distinctive characteristics obtained from native species. Also hybrids, well-adapted to the soil and climate conditions of the productive region of São Paulo State, were the goals of the selection. Most of the new Dutch hybrids brought by immigrant of Holland have showed problems with adaptation.

We also must think if the qualities of the selected hybrids will be acceptable by the customers of European countries, because a big part of our production is sold to these countries. We must know about the behavior of these new varieties in a different climate. Usually there is at least 10°C of difference between our cultivation conditions and the European growing climate, with very low temperatures, or within the houses, with artificial heating and low air humidity.

Would the problems be less formidable for cut flower production?

Table 3 shows a summary of the development of this breeding program.

Tissue Culture

Another project developed at the Flowers and Ornamental Plants Department with *Hippeastrum* is tissue culture multiplication, which is conducted by another researcher of our staff, Carlos de Castro.

The tissue culture program showed encouraging results since the first assays. The last assays resulted in establishment of an effective method of micropropagation of commercial varieties of *Hippeastrum* by meristem or basal plaque.

For the preparation of the vegetative material, eight different sterilizing methods were tested (Table 4).

All the sterilizing methods were good for meristem with only 10% contamination; and also for basal plaque, all the methods gave the same results: 70-80% contamination. Method 1 was chosen because regeneration of the basal plaque explants was higher in this method (25%), while only 5% regeneration occurred in the others. The fungicides and the antibiotics used inhibited the development of the explants but not the meristem, which always showed vigorous growth.

Once the optimal sterilizing method was determined, four different media were tested for micropropagation by meristem and also by basal plaque explants (Table 5).

The best medium for meristem was Number 2, with 100% regeneration; and for basal plaque the best was Number 3, with 25%.

Until now no significant difference was noticed between the varieties. It seems that the time of 2 or 3 years for flowering is similar for those plants propagated by the traditional way. The goal is to obtain virus-free plants, which is possible by meristem culture. But in our country all plantings are made in the field, so the contamination is almost always complete even in just the first growing season.

This method is recommended only for cultures under controlled conditions, free of vector insects.

This research program on *Hippeastrum* is only in its beginning phase, so the extent of the research has yet to be determined. Its ultimate development depends on the efforts needed and upon the results. Every contribution is very welcome to improve this program, especially the breeding and selection of new varieties.

Table 1. *Hippeastrum* Crosses—1983—By Dutilh & Matthes

Number of Crosses	Parental Stock
2	*H. blossfeldiae*×*H. striatum*
4	*H. blossfeldiae*×Hybrid Hippeastrum
1	*H. muesserianum*×*H. stylosum*
1	*H. psittacinum*×*H.* aff. *muesserianum*
3	*H. psittacinum*×*H. puniceum*
1	*H. psittacinum*×*H.* aff. *reginae*
1	*H. psittacinum*×*H.* aff. *puniceum*
1	*H. psittacinum*×*H. striatum* var. *crocatum*
2	*H. puniceum*×*H. atibaium*
4	*H. puniceum*×*H. puniceum*
2	*H. puniceum*×*H.* aff. *puniceum*
7	*H. puniceum*×*H. psittacinum*
4	*H. puniceum*×*H. reginae*
1	*H. puniceum*×*H.* aff. *reginae*
2	*H. puniceum*×*H. striatum* var. *crocatum*
1	*H. reginae*×*H. psittacinum*
1	*H. reginae*×*H. puniceum*
1	*H.* aff. *reginae*×*H. atibaium*
1	*H.* aff. *reginae*×*H. psittacinum*
1	*H. striatum* var. *acuminatum*× *H. striatum*
1	*H. stylosum*×*H. blossfeldiae*
3	*H. stylosum*×*H. psittacinum*
1	*H. stylosum*×*H.* aff. *psittacinum*
1	*Zephyranthes* sp.×*H. stylosum*
1	*Zephyranthes* sp.×*Habranthus* sp.
8	Hybrid *Hippeastrum*×*H. blossfeldiae*
2	Hybrid *Hippeastrum*×*H. psittacinum*
2	Hybrid *Hippeastrum*×*H. striatum*
1	Hybrid *Hippeastrum*×*H. striatum* var. *acuminatum*
2	Hybrid *Hippeastrum*×Unknown *Hippeastrum* species
17	Hybrid *Hippeastrum*×Other Hybrid *Hippeastrum*

Table 2. Crosses on *Hippeastrum* spp.—1986 (Instituto Agronômico, 1989)

Type of Pollination	No. of Pollinations	Effective Pollinations	Flowers Involved	Number of Pods
Cross	298	65	816	304
Selfings	34	20	323	125
Sibs	30	4	200	14

Table 3. Chronology of *Hippeastrum* Breeding Program

Until 1982	*Hippeastrum* collection in Greenhouse
1983	First generation crosses by Julie Dutilh and Luiz Matthes in greenhouse
1986	Second generation crosses by Fernando Tombolato in greenhouse
1987	Transfer of *Hippeastrum* hybrids to field
1988	Second generation crosses by Fernando Tombolato in field and selection of hybrid series from 1983
1989	Multiplication of selected hybrids of 1983 series and selection of 1986 series hybrids

Table 4. Sterilization Methods Tested for *Hippeastrum* Micropropagation (Instituto Agronômico, 1989)

General Preparation: Bulbs were washed in tap water to remove soil; roots were cut off and the basal plaque was carefully cleaned with a small knife.

General Final Washing: Material was rinsed three to four times with sterilized water.

Method 1.
Involved immersion in the following solutions:
70% isopropanol alcohol for 10 seconds, then 20 minutes in a 2% calcium hypochlorite and Tween 20 solution.

Method 2.
Same as # 1, but hypochlorite solution is 1% for 5 minutes.

Method 3.
10% hydrogen peroxide solution, diluted with distilled water, 10 minute soak; 70% isopropanol, 10 seconds; calcium hypochlorite 2%, Tween 20, 30 minutes.

Method 4.
70% isopropanol for 10 seconds; 2% calcium hypochlorite and Tween 20 for 30 minutes; rinse with sterilized water; then antibiotic of benzyl penicillin potassium for 20 minutes.

Method 5.
Same as Method 4 but without antibiotic.

Method 6.
Same as Method 1 but with antibiotic of benzyl penicillin potassium in the medium.

Method 7.
Soak 30 minutes in a solution of Mancozeb 3g/L, Copper 3g/L, Benomyl 0.7g/L; rinse with tap water for 15 minutes; 10 seconds in 70% isopropanol; then 20 minutes in 2% calcium hypochlorite and Tween 20.

Method 8.
Soak 1 hour in 0.5g/L of benomyl; rinse in tap water for 15 minutes; 70% isopropanol for 10 seconds; then 2% calcium hypochlorite and Tween 20 for 20 minutes.

Table 5. Media Tested for *Hippeastrum* Micropropagation

1.	Knudson C (1946) + NAA 0.1mg/L
2.	MS + NAA 0.1mg/L
3.	MS + NAA 0.1mg/L + KIN 0.1mg/L
4.	MS + NAA 0.1mg/L + BA 0.1mg/L

Figure 1. OBSERVATION OF *Hippeastrum* spp. HYBRIDS

Plant no. _____ flowering date of 1st stalk: _____
_____ 2nd stalk: _____
_____ 3rd stalk: _____

Plant Characteristics:
No. of blossoms/stalk: _____
Stalk height: _____ cm
Flowering with leaves ( ) without leaves ( )

Flower Characteristics:

Diameter: cm

Length: cm

Shape: ( ) regular ( ) irregular

Petals: ( ) well expanded ( ) slightly closed ( ) intermediate

Petal width: ( ) wide ( ) narrow ( ) intermediate

Main color: ( ) dark ( ) medium ( ) clear

Stripes: ( ) yes ( ) no

Stripe color: ( ) red ( ) orange ( ) rose ( ) white other: _____

Throat color: ( ) Greenish-white ( ) dark red other: _____

Flower position in relation to stalk:
( ) right angle ( ) sharp ( ) obtuse

General appearance:
( ) not interesting ( ) good ( ) very good

Purpose:
( ) discard ( ) breeding ( ) selection

Observations:

THERMOMORPHOGENESIS IN BULBOUS PLANTS

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ABSTRACT

THERMOMORPHOGENESIS is the periodical growth pattern of bulbous plants under the influence of temperature. Both normal and aberrant morphological phenomena are briefly reviewed.

INTRODUCTION

Bulbous plants show periodical growth patterns. The plants flower at specific times of the year, then produce subterranean storage organs and finally above-ground organs die off. Regrowth starts again in a specific time after a period of apparent rest. Batches of the same variety, growing within certain geographic limits, show an almost synchronous development. It is known that the variation in temperature, according to seasonal conditions, is the most important factor for the control of the periodical growth pattern. The succession of temperature conditions is mostly from high to low to high, corresponding with summer, winter,and spring.

The physiological status of a tissue determines the type of response to the temperature. This means that the exposure of an intact bulb to a certain temperature evokes several effects, since it is composed of bulb scales, one or more generative and/or vegetative buds in different positions, disc tissue and root primordia. The net result of these effects is the periodical development. The characteristic growth pattern of bulbous and tuberous plants has been called thermoperiodicity (TP) (Hartsema 1961).

THERMOPERIODICITY

Recently there has been serious comment on the use of the term thermoperiodicity. Salisbury (1986 and 1987) stated that TP is the phenomenon in which growth and/or development is promoted by alternating day and night temperature on the analogy of photoperiodicity. He suggested to distinguish between a day-type and stage type TP or to find another name.

A better name for the response of plants to the influence of alternating high and low temperatures according to seasonal variation could be thermomorphogenesis. In agreement with the definition of Salisbury, the term TP can be used for those phenomena which occur under the influence of alternating day and night temperatures. From experiments by Kamerbeek (1969), it is known that high night temperatures and lower day temperatures in the greenhouse after planting of the iris bulbs promote the development of the flower bud. A reversed temperature regime results in growth stagnation of the flower bud and leafy plants. Such effects in bulbous plants can be called TP-effects.

Effects of TP on bulbs during dry storage has never been investigated, because of the impracticality on a commercial scale.

PHYSIOLOGICAL STATUS

The type of response of plant tissues to external factors will be determined by its own physiological status. The reaction of meristematic tissue will be an effect on cell division to a certain extent. We know that high temperatures promote leaf and flower formation due to this process. After the formation of new plant organs the temperature exerts its influence on other tissues that are at an incipient stage when a single apex is present. The subsequent response will be an inhibition of the formation of new cells by the apex. The plant system is becoming more and more complex and requires another signal before it can complete its total life cycle. That other signal will be given by another (lower) temperature.

Low temperature will retard cell division, but many biochemical processes will continue thus preparing the plant system for the susceptibility of a new stimulus. A high temperature is required for the second time for the elongation of 'resting' organs. It is not exactly known when the initiating processes are complete.

VARIOUS TEMPERATURE EFFECTS

A. High temperature

For tulips, hyacinths and irises, high temperatures after lifting of the bulbs in summer promote flower formation in the central bud. However in small bulbs the flower formation fails. It has been found that the critical size for flowering can be shifted to smaller bulbs by increasing the temperature and/or extending the period of exposure to higher temperatures.

Prolonged exposure of tulip bulbs to higher temperatures induces leaf and flower formation in axillary buds. Under normal seasonal conditions the temperature drops and cell division ceases before the apices in the axils of the bulb scales reach the stage to respond with flower formation. On the other hand, prolonged high temperature exposures promote the desiccation of flower primordia in the main shoot which senesce.

B. Low temperatures

In tulip bulbs various effects occur under the influence of a low temperature depending on the organ under consideration. First, it causes a preparation for elongation of stems in buds which bear a flower in primordial stage and, second it induces bulbification in vegetative buds (Blaauw *et al.* 1930; Le Nard 1981). This multiple response clearly demonstrates the different reactions of a complex plant system to an integrally administered factor.

In hyacinths the same sort of effects as in tulips can be observed: cooling induces the elongation of the scape and the leaves. Furthermore, low temperatures can reduce the number of leaves, when leaf primordia differentiate to bulb scales instead to foliar leaves. This effect can be observed if the bulbs are exposed to a rather low temperature (3.5 °C.) for long periods after an initial heat treatment at 35 °C. for 3 weeks. The cooling requirement is, however, less than for tulips: shorter periods and less lower temperatures are necessary for normal development.

In irises a high temperature also promotes cell division resulting in an increase of the leaf number. An exposure to temperatures below 20 °C is necessary for the actual flower formation. If the number of leaf primordia does not exceed the number of three, cooling will not result in flower formation, but a new bulb will originate in the center of the mother

bulb. The smaller a bulb, the stronger the bulbification response will be. In other words, small bulbs require more heat to reach the generative state.

Comparing the temperature effects in tulips and irises, we may conclude that at the time of lifting bulbs in summer, the apical meristem of a tulip is in a more advanced physiological state that of an iris. The transition of the apex of a tulip from the vegetative to a potentially generative stage has taken place under field conditions before lifting. The transition in the apex of irises occurs after lifting during the dry storage.

Figure 3. Fifth-level transformed iris flower as a result of the exposure of *Iris* cv. 'H.C. van Vliet' plants to-2° C at the stage of flower formation.

Table 1. Percentage of Hyacinths of cv. 'L'Innocence' with flat scapes (fasciations) and average number of flowers per inforescence as a result of the exposure of the bulbs to 20° C. for 10 days at the onset of flower formation after lifting of the bulbs (Beijer 1936).

Temperature treatment	Flat scapes		Round scapes	
	Percentage	Number of Flowers	Percentage	Number of Flowers
3 weeks 35° C. + 20° C.	8.6	24.3	91.4	15.5
10 days 20° C. + 30° C.	70.4	45.2	29.6	23.7

MORPHOLOGICAL ABERRATIONS UNDER THE INFLUENCE OF THE TEMPERATURE

As mentioned earlier, prolonged exposure of tulip bulbs to high temperatures results in flowering of axillary buds which normally produce daughter bulbs. Abnormal thermal conditions in a specific stage of morphogenesis may cause aberrations of the normal shape. In certain varieties it has been observed that a lower temperature during the process of flower formation results in a higher number of floral organs. The usual number is 15 (6 perianth leaves, 6 stamens and 3 fertile leaves), but up to 24 floral parts were found (Hartsema 1961). Similar phenomena can occur in irises when the temperature drops below zero at the time of flower formation. Fourth, fifth, and sixth level transformation flowers have been found (Figure 3). Pronounced effects have been found in hyacinths after exposure of the bulbs to a 10 °C. lower temperature at the onset of flower formation for two weeks. A fasciated scape will be the result with coincidently increase of the flower number per inflorescence (Table 1.). If at the same developmental stage of the apex the temperature drops to a very low level (0.5 °C) for a long period a branched inflorescence can be formed (Figure 4).

Figure 4. Branched inflorescence of *Hyacinthus* cv. 'L'Innocence' as a result of exposure of the bulbs to 0.5° C for 24 weeks during dry storage beginning when the apex was at the transition to flower formation (Beijer, unpublished)

OTHER MORPHOGENETIC FACTORS

Focussing on the morphological phenomena, the designation of thermomorphogenesis is useful to distinguish from photomorphogenesis and chemomorphogenesis. The similarity between these phenomena is that they are responses to external factors. After exposure of the plant material to external factors the tissue will translate the signals into internal triggers which in turn will activate particular receptors. It is very likely that plant hormones function as such internal triggers. A further analysis of that field will improve our understanding of the morphogenesis of bulbous plants. On the other hand the application of plant growth substances might be useful to replace several temperature or light-induced conditions.

LITERATURE CITED

Beijer, J.J. 1936. De invloed van de schuurbehandeling on de kwaliteit van de hyacint. **Bloembollencultuur** 3, 10, 17 and 24 April.

Blaauw, A.H., I. Luyten and A. M. Hartsema 1930. Verschuiving der periodiciteit. **Kon. Ned. Akad. Wet. Afd. Nat. k.** 2 sectie deel 26, 7: 43-50.

Hartsema, A.M. 1961. Influence of temperature on flower formation and flowering of bulbous and tuberous plants. **Encycl. Plant Physiology** 16: 123-167.

Kamerbeek, G.A. 1969. Influence of light and temperature on flower bud development in bulbous irises (*Iris* cv. Wedgwood) and lilies (*Lilium* cv. Enchantment). In: Proc. Symp. Flower Regulation in Florist Crops. Vollebek. 12-16 August 1968. The Hague: 175pp.

Le Nard, M. 1981. Physiology and storage of bulbs: concepts and nature of dormancy in bulbs. In: Post-harvest physiology and crop preservation. M. Lieberman ed., Plenum, New York and London, 191-230pp.

Salisbury, F.B. 1986. Vernalization and photoperiodism. In: A.H. Halevy ed. **Flowering Newsletter** 3:14-16.

Salisbury, F.B. 1987. Terminology in the field of flowering. In: A.H. Halevy ed. **Flowering Newsletter** 4:16-22

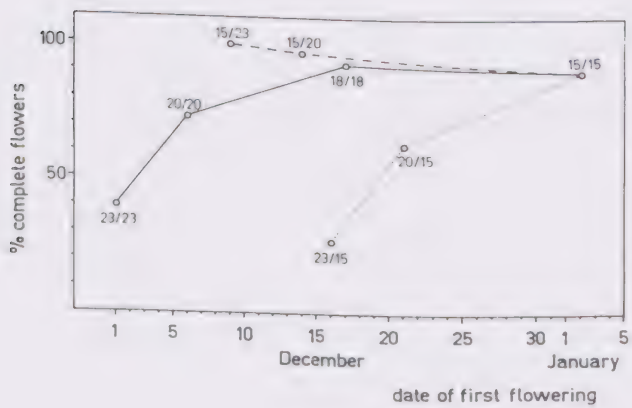

Figure 1. Promotive effect of high night and low day temperatures on the development of flower buds of *Iris* cv. Wedgewood plants (Kamerbeek 1969).

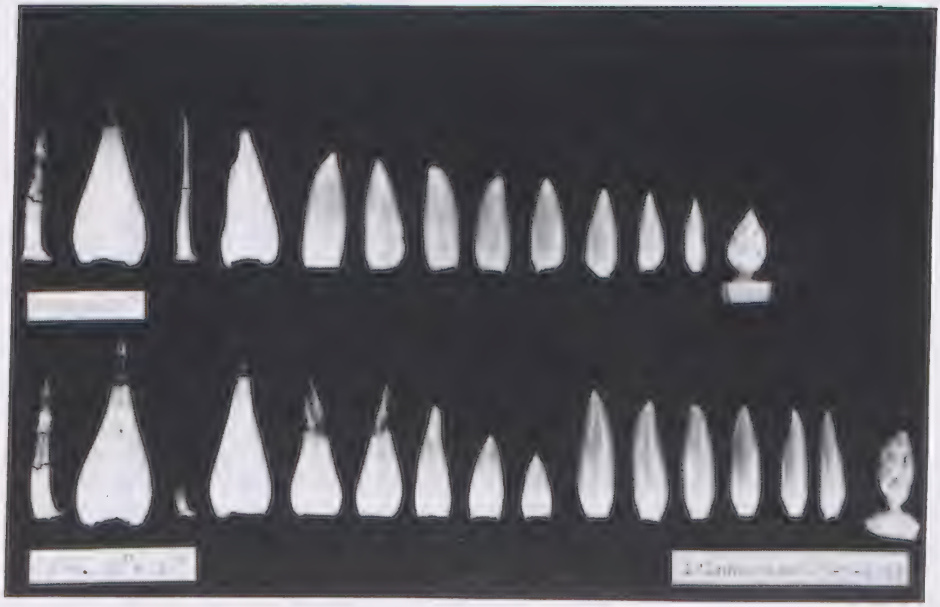

Figure 2. Reduction of the number of leaves and increase of the number of bulb scales of *Hyacinthus* cv. 'L'Innocence' under the influence of a 27-week period of storage at low temperature (3.5° C) after a heat treatment at 35° C for 3 weeks (Beijer, unpublished).

HYBRID *RANUNCULUS* RESPONSE TO COLD TREATMENTS ON CORM SPROUTS

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ABSTRACT

COLD treatments on hybrid *Ranunculus* sprouts, which had emerged from the corms, were applied for different lengths of time. The effects on productivity and on precocity of production were evaluated. Cold treatments maintained at 10 °C or applied after sprout emergence seem more suitable than those at 2 °C on hybrid *Ranunculus* cv. 'Grazia' of local production. A critical survey of forcing procedures and their applicability related to cultural techniques on hybrid *Ranunculus* in Italy is reported.

INTRODUCTION

Hybrid *Ranunculus* is a popular crop for cut flowers of the Sanremo area in Italy. The seedlings are planted in winter for spring production of the flowers and for the production of the rhizomes in the following summer. The rhizomes are then utilized in the early cut flower production.

The *Ranunculus* species in nature blooms in the spring. However, the market is interested in an early production owing to the presence of too many other species in spring.

Studies on the biological cycle and on the cultural techniques on hybrid *Ranunculus* were carried out with the aim of increasing earliness. Among cultural techniques, the shifting of planting dates is limited by the high soil temperatures in summer, which preserve the corms in a dormant state (Farina *et al.* 1986).

Forcing procedures with cold treatments were applied too on corms kept in moist peat to improve sprouting (Volpi 1975; Dalla Guda and Volpi 1985) and to obtain an early production of cut flowers in November-December (Farina and Dalla Guda 1987).

In these trials the effects of cold treatments on sprouts which had just emerged from the rhizomes were tested. The aim was to reduce the duration of the cold treatment without harming early production.

MATERIAL AND METHODS

Hybrid *Ranunculus* cv.'Grazia', of local variety, characterized by the doubling of the flowers, were kept at 18 °C in moist peat for 4 days until sprout emergence on the corms. The temperature was then reduced to 2 °C in the first trial and to 10 °C in the second trial and maintained at these values for 10-20-30 days.

Other rhizomes were kept in moist peat at 2°C or 10°C for 30 days.

The treated rhizomes, together with the dried corms, were planted in open air at the same time. Experimental data are reported in Table 1.

The average number of sprouts on corms and their size were observed after cold treatments.

The quality and the precocity of production of treated and untreated rhizomes were compared.

RESULTS

The average number of emerged sprouts depends on length of the cold treatments and temperature. Both the cold temperatures or being maintained at 2°C or the one applied after sprout emergence seem unfavorable. Sprout size was also reduced by low temperature. Data are reported in Table 2.

Treated corms gave an earlier production than the dried ones. The days to the opening of the first three flowers were always less for treated corms.

The productivity of the first grade flowers too was not influenced by any of the treatments. Data are shown in Tables 3 and 4.

Cold treatments maintained at 10°C or applied after sprout emergence seem more suitable than those at 2°C on hybrid *Ranunculus* cv. 'Grazia' of local production.

The best results on hybrid *Ranunculus* cv. 'Grazia' were obtained by applying 10°C maintained for 30 days on corms kept in moist peat. All the other treatments were less effective to give the same production when the length of the period at low temperature was reduced.

DISCUSSION

Treated corms maintained in most peat at 10°C for 30 days gave the first flower after 125-126 days, about two months before the untreated ones (dried corms). The presence of the sprouts on corms before planting is not so important; however, it is to be noted that the length of the cold treatments is of the greatest importance. By increasing the length of time at low temperatures, the days to flowering decreased.

Early production (November-February), may be obtained by utilizing the forcing procedures together with different cultural techniques: the reduction of the soil temperature and the use of artificial light.

LITERATURE CITED

Dalla Guda, C. and L. Volpi 1985. Prove sperimentali sul germogliamento di rizomi di ranuncolo (ibridi 'Grazia', a diverse temperature. **Ann. Ist. Sper. Flor.** XVI:1-12.

Farina, E. and C. Dalla Guda 1987. La programmazione colturale del ranuncolo ibrido. **Atti Giornata S.O.I. Scicli**: 91-101.

Farina, E., T. Paterniani and C. Dalla Guda 1986. Effecto dell'epoca di impianto, della preparazione dei rizomi, del fotoperiodo sulla produzione precoce del ranuncolo ibrido. **Ann. Ist. Sper. Flor.** XVII: 13-24.

Volpi, L. 1975. Osservazioni sulia fioritura del ranuncolo a seguito di trattamenti termici e di piantagioni scalari. **Ann. Ist. Sper. Flor.** VI: 15-26.

Table 1. Hybrid *Ranunculus* cv. 'Grazia'. Experimental data.

	1st trial	2nd trial
Colours	White-pink-red	White-yellow Pink-red
Planting date	9.18.1986	9.16.1987
Treatments A B C D	18 °C for 4 days Dried corms (untreated) 10 °C for 30 days 2 °C for 30 days	18 °C for 4 days Dried corms (untreated) 10 °C for 30 days
	A+2 °C for 10 days A+2 °C for 20 days A+2 °C for 30 days	A+10 °C for 10 days A+10 °C for 20 days
Cell (corms)	50	20
Cell (field)	20	30

Table 2. Hybrid *Ranunculus* cv. 'Grazia'. Average number and size of sprouts which had emerged from the corms.

Treatments	Average No. of sprouts after			Size (cm) after		
	DAYS					
	10	20	30	10	20	30
10 °C	3.77	3.90	3.79	0.21	1.73	3.88
2 °C	1.26	1.89	2.25	0.10	0.15	0.15
A+2 °C	2.81	2.37	4.00	0.10	0.38	0.38
A+10 °C	3.20	3.77	3.80	0.65	2.20	5.50

Table 3. Hybrid *Ranunculus* cv. 'Grazia'. Number of days from planting to the opening of the first three flowers.

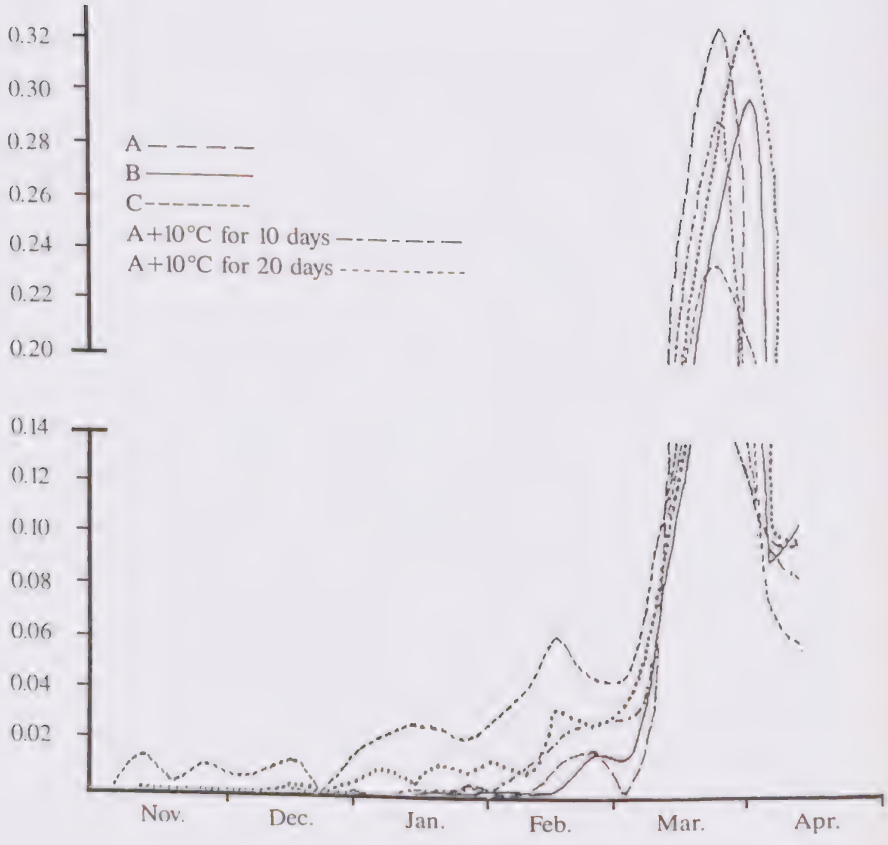
Days to flowering	1st Trial							2nd Trial				
	TREATMENTS											
	A	B	C	D	A+2 °C for			A	B	C	A+10 °C for	
					10 Days	20 Days	30 Days				10 Days	20 Days
1st flower	189.70 bcd	194.59 d	126.61 a	170.27 b	190.23 cd	181.40 bcd	174.25 b	174.59 c	176.16 c	125.15 a	169.13 bc	155.66 b
2nd flower	198.73 bc	203.27 c	160.78 a	187.06 b	199.83 bc	193.58 bc	188.25 b	183.60 c	185.65 c	147.83 a	177.65 bc	170.10 b
3rd flower	203.95 bc	209.57 c	180.92 a	193.32 b	204.23 bc	198.07 b	195.48 b	188.27 c	189.06 c	158.89 a	179.13 bc	177.31 b

In each trial, means of the same row followed by the same letter do not differ significantly. (P =0.05 Duncan Test)

Table 4. Hybrid *Ranunculus* cv. 'Grazia'. Effects of cold treatments on flower production (November-April).

Plant yield (flowers)	1st Trial							2nd Trial				
	TREATMENTS											
	A	B	C	D	A+2 °C for			A	B	C	A+10 °C for	
					10 Days	20 Days	30 Days				10 Days	20 Days
Total	8.85	8.79	11.12	9.33	8.13	10.30	8.84	9.76	8.78	10.54	9.67	9.67
First grade	5.10	5.63	7.88	6.69	4.47	6.50	5.24	4.50	4.54	5.46	4.77	5.56

Graph 1. Hybrid *Ranunculus* cv. 'Grazia'.
Flower production. (2nd Trial)
flower plants -1 days-1



ABSTRACTS

HERBERTIA 45(1 & 2)—1989

INDUSTRIALIZATION AND HYBRIDIZATION IN DUTCH *HIPPEASTRUM* GROWING

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ABSTRACT

HIPPEASTRUM culture in the Netherlands has been developing to the level of a high tech crop until 1980. After that time the relative economic value has been decreasing dramatically due to inflexibility of the crop under Dutch growing circumstances and lack of new varieties.

Originally the culture cycle ran from October to December plantings; and September–October harvests, resulting in products which did not flower in time for Christmas.

Trials have been made with June plantings and 13-14 months continuous culture. Results on a commercial scale are promising.

The breeding project from the growers co-operation "The Amaril" is aiming to combine these two elements in the large flowering *leopoldii* varieties and resistance against *Fusarium*. The first element, flexibility of the crop, can be defined by: ability to be grown under low light conditions, at a moderate temperature without perishing leaves and a continuous bud production.

The second element, new varieties, can be defined by: varieties with stronger stems, four flowers at the first stem and bud formation in a smaller sized bulb.

To reach this goal, varietal research under the described cultural circumstances and crossed programs with the selected parents have been carried out.

Variation on the mentioned characteristics is quite large inside the current grown varieties.

ALSTROEMERIA IN CHILE

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ALSTROEMERIA (Alstroemeriaceae) is a uniquely South American genus. There are two centers of distribution, one of the west side of the Andean chain, mainly in Chile with about 30 species and the other ones in Brazil, probably with less species. The genus was founded in 1762 by Linnaeus. The Alstroemerias are herbaceous perennials with fleshy root-tubers and a rhizome bearing sterile and fertile stems. The other main features are the often resupinate leaves and the more or less zygomorphic, brightly colored, spotted flowers mostly in an umbel-like inflorescence. The fruit is a capsule. Because of its attractive flowers *Alstroemeria* is of great interest for horticulture.

Alstroemeria grows in quite different habitats. Some Brazilian species live in swamps, the Chilean ones occur from the coast up to the highest Andes, from the dry north to the moist south of Chile. Most of them can be found in Central Chile. The distinction of the different species is quite difficult; some of them are very variable, others hybridize. In Chile there can be found quite isolated species like *A. graminea*—and *A. hookeri* group. The differentiating characters are among others the leaves of the sterile stem, the indument and mainly form, size, colour and pattern of the flower. The number of chromosomes seems to be throughout $2n = 16$. The relations of the species are difficult to understand. Probably future cytological research will help to clear the problems.

LYCORIS SPECIES AND HYBRIDS

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THE genus *Lycoris* (Amaryllidaceae), which consists of about twenty species distributed in Eastern Asia, is an interesting group from the stand points of ornamental horticulture and botany. The species and hybrids of this genus have a high potential as a horticultural crop because of their graceful blooms, variations in flower color and ease of culture. Until quite recently little has been known concerning the value of this genus among horticulturists. Now several breeders in Japan, however, intend to develop the potential of this genus. On the other hand, many karyomorphological studies have been attempted on this genus. Using karyotype analysis, the evolution and phylogeny of the genus can be hypothesized. The presentation will illustrate the characteristics of the genus and present the enchantment of the species and hybrids by the use of several color photographic slides.

CONTROL OF FLOWERING IN *LILIUM* — A REVIEW

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ABSTRACT:

CONTROL mechanisms of flowering in various species of *Lilium* are reviewed in relation to bulb vernalization and shoot photoperiod. Flowering of *L. longiflorum*, *L. speciosum* and *L. lancifolium* is accelerated by both bulb vernalization and shoot photoperiod. Flowering of *L. elegans* is accelerated only by bulb vernalization and long day photoperiod treatment is not effective if given to shoots after emergence. Although there are great differences in bulb vernalization temperatures among *L. elegans* cultivars, optimum bulb vernalization temperature is about 5 °C. Any treatment that accelerates flowering of *L. longiflorum*, *L. speciosum* and *L. lancifolium*, regardless of bulb temperature and shoot photoperiod treatment, reduces flower bud number. However, bulb vernalization increases the number of flower buds in *L. elegans*. The difference between *L. elegans* and other species is that flower bud initiation in *L. elegans* is completed within 3 to 21 days upon completion of cold treatment. Current research projects with *L. elegans* at the United States Department of Agriculture will be discussed.

INTRODUCTION

About 100 species in the genus *Lilium* area reported. However, *L. longiflorum*, commonly known as the Easter lily, and *L. elegans*, commonly known as the Asiatic hybrid lily, have been grown extensively as potted plants or for cut flowers. Growth and flowering physiology of the Easter lily as influenced by bulb vernalization and shoot photoperiod have been investigated extensively. However, information on the Asiatic hybrid lily and *L. speciosum*, commonly known as the Oriental lily, is not readily available.

Research on the forcing of the Asiatic hybrid lilies in the Florists and Nursery Crops Laboratory, Beltsville, Maryland has been focused (a) to identify optimum bulb vernalization temperatures for each cultivar, (b) to investigate the amount of low temperature stimulus (c) which is accumulated in the bulb before harvest, and (d) to relate flower bud initiation with respiration profile and to the changes in the level of carbohydrates in the shoot apex.

In this paper, literature on *L. longiflorum*, *L. speciosum*, *L. lancifolium*, *L. hansonii* and *L. distichum* is reviewed and research projects with *L. elegans* are briefly described. Due to the vase amount of literature on *L. longiflorum*, information will be limited to publications by the author without listing extensive literature of others.

CONTROLLING MECHANISMS OF FLOWERING

Before discussing flowering responses controlled by bulb vernalization and shoot long day photoperiod, it is important to define the terms, dormancy and maturity, in the lily bulb in controlling growth and flowering.

Dormancy has been defined as a temporary arrest in growth of the shoot apex of the lily bulb. When harvested early after flowering (July), bulbs are considered dormant as compared to bulbs harvested late in the season (October). When bulbs are harvested early, they are considered to be dormant and consequently not mature. Those bulbs cannot perceive flowering stimulating treatments from low temperatures. Dormancy is generally expressed by the speed of shoot emergence after planting; while maturity is expressed by an early and uniform shoot emergence and also by flowering response to bulb vernalization. Some researchers have used dormancy as an indirect measure of the stage of maturity in the Easter lily. However, in *L. longiflorum*, dormancy, judged by the speed of shoot emergence, cannot be used to define maturity since factors controlling dormancy are not translocated through the basal plant and factors controlling maturity are so translocated (Table 1).

Table 1. Translocation of dormancy and maturity factors in *L. longiflorum* 'Nellie White' bulbs (modified after Roh and Wilkins 1977b).

Number of Weeks at 5 °C	Scale Treatment* Left	Right	Days to Flowering Left	Right	Number of Flowers Left	Right
0	+M+D	+M+D	54	56	6.6	6.6
	−M−D	−M−D	29	30	1.4	1.2
	+M+D	−M−D	53	33	6.4	6.8
4	+M+D	+M+D	60	60	6.0	6.5
	−M−D	−M−D	58	56	1.0	1.0
	+M+D	−M−D	49	50	6.2	2.6

* — Left and right indicate two shoots from one double-nose bulb that has two growing points. Plus (+) and minus (−) indicate that mother (M) and daughter (D) scales were attached or removed respectively, from the basal plate.

When one considers the native growing areas of this species, it is questionable whether *L. longiflorum* bulbs possess dormancy since shoots emerge at temperatures higher than 21 °C. Shoot emergence of the Easter lily is delayed by bulb vernalization treatment (when the number of days to shoot emergence was counted from the beginning of vernalization, but not from the end of vernalization treatment). When bulbs are harvested from the West Coast of the United States, they emerge faster as 21°C, as compared to 16 °C and are able to flower with long day photoperiods given after shoot emergence at temperatures lower than 21 °C. Therefore, dormancy could not be used to measure or determine the maturity of the bulbs.

With *L. elegans*, *L. hansonii*, *L. lancifolium* and *L. distichum*, shoot emergence can be delayed for 3 to 6 months when bulbs are harvested immediately after flowering and are placed at 21°C without bulb vernalization. Therefore, to accelerate flowering, dormancy must be broken to promote shoot emergence.

Another important factor to consider is the time of flower bud initiation between the species *L. longiflorum*, *L. speciosum* and *L. lancifolium*, and the species *L. elegans*, *L. hansonii* and others. Flower bud initiation in the former group occurs after shoot emergence and in the latter group before shoot of *L. longiflorum* can replace bulb cold treatment. However, shoot photoperiod treatment in *L. elegans* is not effective in replacing bulb vernalization treatment.

THE EFFECT OF BULB VERNALIZATION

Group A. *Lilium longiflorum*, *L. speciosum* and *L. lancifolium*

In these species, bulb vernalization accelerates flowering, but decreases the number of flower buds. In *L. lancifolium*, shoot emergence of bulbs that received 42 days of 5 °C was about 60 days earlier than that of bulbs without 5 °C treatment. Flowering was accelerated by about 50 days and flower numbers were reduced by about 4 with bulb vernalization. Long day photoperiod treatment also accelerated flowering in non-vernalized bulbs as much as 32 days (Table 2). Similar results were observed in *L. longiflorum* and *L. speciosum*. It is questionable whether or not *L. longiflorum* posses true dormancy as compared to a deep dormant state in bulbs of *L. speciosum* and *L. lancifolium*.

Table 2. Flowering date and number of flowers of *L. lancifolium* as influenced by bulb vernalization and shoot photoperiod (modified after Roh *et al.* 1979).

Number of Weeks at 5 °C	Photoperiod	Flowering Date	Number of Flowers
0	Short Day	June 8	12.8
	Long Day	May 6	8.0
6	Short Day	April 18	8.5
	Long Day	April 15	7.6

Group B. *Lilium elegans*, *L. distichum* and *L. hansonii*

In these species, bulb vernalization accelerated flowering and also increases the number of flowers as compared to *L. longiflorum* and *L. lancifolium*. Further, these three species may require at least 4 to 8 weeks of optimum bulb vernalization to break dormancy and to induce early flowering. The optimum bulb vernalization temperature for many *L. elegans* cultivars is near 5 °C, although the upper temperature limit for different cultivars differs significantly. For example, when 'Inferno' bulbs were harvested from the West Coast, they flowered even when bulbs were stored at 21 °C. In fact, they flowered earlier than bulbs stored at temperatures ranging from 0 °C to 15 °C. However, bulbs or cultivars, like 'Sunray', 'Connecticut Lemonglow' or 'Red Carpet' required vernalizing temperatures below 12.5 °C.

Lilium distichum bulbs require at least 8 weeks of 5 °C to break dormancy and flower (Table 3). The number of flowers is increased by half when bulb vernalization is increased from 8 to 10 weeks. *Lilium hansonii* bulbs that received 6 weeks of 5 °C did not emerge for 180 days, which indicates that they were in deep dormancy, as compared to *L. longiflorum*.

Table 3. Effect of 5 °C on the number of leaves and flowers of *L. distichum* (modified after Kim 1987).

Number of Weeks	Number of Leaves	Number of Flowers
6	1.0	0
8	9.8	1.5
10	15.0	2.0

EFFECT OF LONG DAY PHOTOPERIOD

Group A. *Lilium longiflorum*, *L. lancifolium* and *L. speciosum*

Flowering of these three species is accelerated by a long day photoperiod when given to shoots after emergence. Long day treatment given to bulbs is not effective in promoting flowering, but illuminating daughter scales, where dormancy factors are assumed to be present, accelerates shoot emergence. Once again, dormancy cannot be used to measure the level of maturity.

Lilium lancifolium and *L. speciosum* bulbs require some cold treatment before shoots can emerge. Temperature requirements in these two species are not well investigated as compared to those of *L. longiflorum*. Flowering of the Easter lily by long day photoperiod depends on the condition of bulb vernalization and forcing temperature. For example, in non-vernalized bulbs, long day treatment is effective only when forcing temperature area lower than 21°C, which is the upper limit of vernalizing temperature. However, when bulbs received on week of vernalization, long day effect could be seen even at temperatures higher than 21°C. Flowering of *L. longiflorum* is thus accelerated by giving insufficient bulb vernalization, for example 3 weeks of cold, followed by 3 weeks of long day treatment after shoot emergence, so that the total length of the flowering inductive treatment period is 6 weeks (Table 4). Both bulb vernalization and shoot photoperiod treatments accelerate flowering and reduces the number of flowers in *L. lancifolium*, *L. speciosum* and *L. longiflorum* (Tables 2 and 4).

Table 4. Relationship between bulb vernalization and shoot photoperiod on flowering of *L. longiflorum* 'Nellie White' (modified after Roh and Wilkins 1973).

Number of Weeks of 5°C	LD	Days to Flower	Number of Flowers
0	0	195	13.0
6	0	162	6.7
0	6	147	6.2
3	3	148	6.7

Group B.

In *L. elegans*, long day treatment given to shoots does not accelerate flowering in many hybrids (Table 5). One of the reasons is that flower bud initiation is completed before shoots emerge from the noise of the bulb or before shoot emergence from the soil level.

Table 5. Flowering of *L. elegans* 'Inferno' influenced by bulb vernalization and shoot photoperiod (Roh 1984 and unpublished data).

Number of Weeks at 5°C	Photoperiod	Days to Flower	Number of Flowers
0	Short Day	86	4.3
	Long Day	83	4.8
8	Short Day	70	5.6
	Long Day	69	5.3

CURRENT RESEARCH PROJECTS AT THE U.S.D.A

It is well known that forcing of the Easter lily differs year after year although the greenhouse forcing practices may not differ significantly. Most of the yearly variations are attributed to the amount of field temperatures that are accumulated in the bulbs before they are harvested. If temperatures in the production field are too low, bulbs may not require 6 weeks at 5°C.

However, it is difficult to measure the number of hours of low temperatures which bulbs receive prior to reaching the greenhouse forcers. Therefore, one of the needed research areas is finding a marker system for bulb maturity. It is proposed that a respiration profile could be used. The time of flower bud initiation and the time of stem elongation after completion of flower bud initiation might be pinpointed, if a respiration profile could be developed.

Two other projects are on the controlling mechanism of flower bud abscission in *L. elegans* and on flower senescence in *L. longiflorum*. Research focuses on carbohydrate metabolism in various parts of the floral organs. Some of the results on respiration profile in relation to flower bud initiation and development, as well as bud abscission and flower senescence has been studied.

LITERATURE CITED

Lilium longiflorum

De Hertogh, A. A., A. N. Roberts, N. W. Stuarts, R. W. Langhans, R. C. Linderman, R. H. Larson, H. F. Wilkins and D. C. Kiplinger 1971. A guide to terminology for the Easter lily (*Lilium longiflorum* Thunb.). **HortScience** 6:121-123.

Lin, W. C. and H. F. Wilkins 1973 Influence of bulb harvest dates and temperature treatments on growth and flowering of *Lilium longiflorum*. **J. Amer. Soc. Hort. Sci.** 100(1):6-9.

Roh, S. M. and H. F. Wilkins 1977a. The effect of bulb vernalization and shoot photoperiod treatments on growth and flowering of *Lilium longiflorum* Thunb. cv. 'Nellie White'. **J. Amer Soc. Hort. Sci.** 102(3):22-235.

_____ 1977b. The physiology of dormancy and maturity of *Lilium longiflorum* Thunb. cv. 'Nellie White'. **J. Kor. Soc. Hort. Sci.** 18(2):194-202.

Weiler, T. C. and R. W. Langhans 1968. Effect of photoperiod on the vernalization requirement of *Lilium longiflorum* Thunb. cv. 'Ace'. **Proc. Amer. Soc. Hort. Sci.** 93:630-634.

Lilium speciosum

Ohkawa, K. 1977. Studies on the physiology and control of flowering in *Lilium speciosum rubrum*. Special Bulletin, Kanagawa Hort. Expt. Sta. July, 1977. 73pp. (in Japanese with English summary).

Lilium elegans

Suzuki, M. 1974. Studies on the forcing lilies. I. A study on the forcing of *Lilium elegans* Thunb. **Bull. Veg. and Ornam. Crops Res. Sta**, Ser. A 1:185-214.

Roh, M. S. 1981. Response of Mid-Century hybrid lilies to bulb vernalization and shoot photoperiod. **HortScience** 20(4):710-713.

Pergola, G. and M. A. Roh 1977. Relationship between flower bud initiation and respiration in Asiatic hybrid lily bulbs. **Acta. Hort**. 205:241-247.

Lilium lancifolium

Roh, M.S. 1979. Various factors influencing the growth and flowering of *Lilium lancifolium* Thunb. **J. Kor. Soc. Hort. Sci.** 20)1):72-83.

_____ 1982. Dormancy and maturity in the bulbil of *Lilium lancifolium*. 3. The influence of growth regulator treatment on the growth and flowering responses. **J. Kor. Soc. Hort. Sci.** 23(1):59-63.

Lilium distichum

Kim, S. H. 1987. Ecology, breakdown of bulb dormancy and scale propagation of *Lilium distichum* native to Cheju Island, Korea. MS Thesis, 42pp. Cheju National Univ., Cheju, Korea (in Korean with English summary).

Lilium hansonii

Roh, S. M., D. Y. Yeam and Y. J. Kim 1978. Native bulb materials in the wild and their production for the cultivation as a floricultural crop. I. Survey and bulb production. **J. Kor Soc. Hort. Sci.** 19(2):129-146 (in Korean with English summary).

INFLUENCE OF CULTURAL ENVIRONMENT ON *IN VITRO* PROPAGATION OF TULIPS

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TULIPS (*Tulipa gesneriana*), long considered an essential component of flower gardens, are becoming associated with spring holidays as cut flowers or potted plants. Conceivably, the use of tulips as a glasshouse crop could be increased if new cultivars were introduced regularly. However, release of a new cultivar may require more than 20 years (Eijk 1989). Flowering usually occurs 5 years after planting the seeds, and, after selection, at least 15 additional years are needed for vegetative propagation of enough bulbs for trials and release.

Considerable research on *in vitro* propagation of tulips has been conducted in an attempt to shorten bulb production time. Two main approaches appear in the literature. One approach uses nodal tissue of the floral axis of 'Merry Widow' bulbs explanted on a modified MS (Murashige and Skoog) medium containing NAA (1-Naphthaleneacetic acid;) and BA(6-Benzylaminopurine) (0.001g/L each), with 30g/L sucrose, and a pH of 6.1 (Wright and Alderson 1980). Before explanting, the floral axes are allowed to elongate by storing bulbs at 17°C. Cultures are incubated at 20°C under a 16 hour photoperiod.

The second approach uses the basal section of the scales of 'Apeldoorn' bulbs as the explant source on a modified MS medium containing 2,4-Dichlorophenoxy acetic acid and kinetin (0.001g/L each), with 20g/L sucrose, and a pH of 5.6 (Nishiuchi 1979). Scales are explanted immediately after bulb harvest and cultures are incubated at 23°C under continuous light.

Despite differences in techniques, shoots (leaves) appear after 8-12 weeks. Bulbs would develop at the base of these shoots, provided that explants were incubated at 4-5°C for 2-4 months and then transferred to culture medium containing an increased concentration of sucrose and a decreased concentration of plant growth substances (Nishiuchi 1979, 1980; Wright and Alderson 1980; Rice *et al.* 1983).

For our first attempt at *in vitro* culture, flowering-sized 'Apeldoorn' bulbs, 10-11cm diameter, were imported from South Africa and non-flowering-sized 'Apeldoorn' bulbs were imported form the Bulb Research Centre, Lisse, Netherlands. Half of each group of bulbs was stored at either 5° or 20°C for 0, 1, 4, or 8 weeks. After storage, bulbs were washed and placed in a solution of mercuric chloride (0.2g/L) for one hour. Floral axes and scales were removed from the bulbs and placed in a 0.5% NaOCl solution with 0.5ml/L Tween 20 for 20 minutes then rinsed 3 times with autoclaved distilled water.

The floral portion of an excised floral axis was discarded, and the remainder bisected longitudinally, forming 2 explants. Scales were cut into three sections, ie. top, middle and bottom, and sections were cut into 2 more 5×5mm pieces.

Each explant was placed into a vial (25×95mm) containing 10ml of medium. Three media were tested. The first was an MS medium containing 0.5g/L casein hydrolysate, with NAA and BA at 0.001g/L each, at a pH of 6.1 (Wright and Alderson 1980). The second was an MS medium containing 2g/L casein hydrolysate, with 2, 4-D and kinetin at 0.001g/L each, at a pH of 5.6 (Nishiuchi 1979). The third was an MS medium with 0.5g/L casein hydrolysate, containing 2, 4-D at 0.001g/L, at a pH of 6.1. Sucrose concentrations of 20 , 40, and 60g/L were tested in each medium. Vials were placed at 20° or 24°C in either continuous light or dark and evaluated after 2 or 4 months.

Regardless of the source of the bulbs, no explants produced organized structures *in vitro*. Scale tissue from flowering-sized bulbs turned brown, but explants from scale tissue nearest the basal plate of non-flowering-sized bulbs swelled and infrequently formed callus. Explants from floral axes merely elongated, perhaps because they were not divided into nodal sections (Wright and Alderson 1980).

Although mercuric chloride is considered a harsh surface-disinfestation agent and could have damaged tissues (Miller and Gould 1967), it did not control fungal contamination. Therefore, the use of mercuric chloride was discontinued.

Our second attempt at *in vitro* culture used flowering-sized 'Apeldoorn' and 'Merry Widow' bulbs (10-11cm diameter) imported from Hokkaido University of Education, Asahikawa, Japan. A 5×2 factorial experiment with 5 replications was designed. Factors included cultivar ('Apeldoorn' or 'Merry Widow'), preculture bulb-storage time (36 or 63 days), preculture storage temperature (17 or 20°C), culture medium (Nishiuchi 1979 or Wright and Alderson 1980), and cultural temperature (20 or 24°C).

After storage, the floral axis and second scale from the floral axis were removed from each bulb, placed in a solution of 0.5% NaOCL with either Tween 20 or Liqui-nox for 20 minutes, and then rinsed 3 times with autoclaved distilled water. Floral tissues were discarded and the remaining axis was dissected into the 4 nodes. The bottom third of the second scale from the floral axis was removed and cut into 5×5mm pieces. The remainder of the scale was discarded. Each nodal section of the floral axis and each scale piece was placed into a vial (25×95mm) containing 10ml of either the Nishiuchi (1979) or the Wright and Alderson (1980) medium. Cultures were placed in the dark at either 20 or 24°C and evaluated after 1, 2, and 3 months.

Bulb-scale tissue, regardless of cultivar, turned brown without producing organized structures. Our methods for scales explanted on the medium Nishiuchi (1979) used were as identical to his as possible, except for incubation in darkness rather than in continuous light. However, organized structures did not appear in our first attempt, when bulb-scale explants were incubated in continuous light on this same medium. Our inability to duplicate Nishiuchi's results is difficult to explain. Perhaps our bulbs were physiologically altered as a result of transport and handling during importation.

Explants from the floral axis produced leaf-like structures (shoot-like structures as photographed by Nishiuchi 1979, and Wright and Alderson 1980) as soon as 1 month after initiation of culture, regardless of cultivar (Table 1). These leaf-like structures have the appearance of solid cylinders when dissected and exhibit no evidence of nodes (Figure 1). Our results are similar to those reported by LeNard *et al.* (1987), who also incubated explants in the dark and observed leaf-like organs in one month.

Neither bulb storage temperature, nor cultural temperature affected the number of explants producing organized structures. Cultural temperature of 20°C (Wright and Alderson 1980) or 23°C (Nishuichi 1979) have been reported as optimum for *in vitro* culture, but we found no difference. Although Wright and Alderson (1980) observed that node 1 (the node nearest

the basal plate) produced more organized structures than the other nodes of 'Merry Widow' floral axes, we noticed no difference due to nodal position. More recently, Taeb and Alderson (1987) questioned the superiority of node 1 in production of organized structures.

Floral axes explanted from bulbs stored 63 days produced more cultures forming leaf-like structures than those from bulbs stored 36 days (Table 1). Bulb age has been reported to affect *in vitro* production of shoots (Wright and Alderson 1980; LeNard *et al.* 1987). The floral axis elongated during storage, from about 20 mm at 36 days to about 25mm at 63 days. Perhaps changes in the floral axis during elongation affect *in vitro* response.

The medium containing NAA and BA (0.001g/L each) produced the most explants with leaf-like structures, regardless of preculture storage or month of data collection (Table 1). Explants on the 2,4-D and kinetin (0.001g/L each) medium developed leaf-like structures, but only after 2 months. These explants appeared to form callus first, then organized structures, while explants on the NAA-BA medium developed organized structures directly.

After 3 months of culture, all explants were placed at 5 °C in the dark for 4 months, then returned to 24 °C in the dark and evaluated after 2 months. Bulbs developed at the base of the organized structures in about 10% of the explants. However, if the explants lacked organized structures before incubation at 5 °C or if explants with shoot-like structures were not placed at 5 °C, no bulblets formed. This method of bulb production, from organized, shoot or leaf-like structures, has been reported (Nishiuchi 1980; Rice *et al.* 1983; LeNard *et al.* 1987).

The growing season for tulips in the native habitat has a warm fall, cold winter, and a warm spring thermocycle. With commercial forcing of tulips, bulbs are potted and placed at 17-20 °C (fall) for initiation and development of roots and flowers (DeHertogh *et al.* 1983). Next, an extended 2-9 °C (winter) period is needed, so that elongation of the floral axis and flowering can occur when the bulbs are placed at 17-20 °C (spring).

Initiation and development of daughter bulbs (LeNard and Cohat 1968) and bulbs from excised tulip embryos (Niimi 1978) also follow the natural thermocycle. The inductive process requires low temperatures (winter) and organizes the bulb primordium (LeNard and Cohat 1968). Manifestation of the bulbing process is more rapid at higher temperatures (spring). When held continuously at 4 °C, embryos do not form bulbs, but a transfer to 24 °C after 4 °C promotes development of a bulb primordium (Niimi 1978). Niimi found that differentiation of the bulb primordium depended upon the duration of exposure to 4 °C.

For *in vitro* culture of tulips, Nishuichi (1979) and Wright and Alderson (1980) place explants in a warm environment (20-23 °C) for shoot development, then in cold (4-5 °C) for initiation of the bulbing response, and, finally, in a warm environment (20-25 °C) for bulb development. This thermocycle is similar to that which leads to daughter bulb production in nature and bulbs from excised embryos, except that the *in vitro* methods result in shoot formation before bulbs, rather than bulb formation directly on the explants.

In the next attempt at *in vitro* culture, we tried to produce bulbs directly from the explants, without the intervening formation of leaf-like structures. 'Apeldoorn' bulbs, 10-11cm diameter, were imported from the Bulb Research Centre, Lisse, Netherlands. The bulbs were stored at 20 °C in the dark until the floral axis had elongated to at least to 25mm. After disinfestation, the floral axes were removed and placed in a solution of 0.5% NaOCL with 0.5ml/L Liqui-nox for 20 minutes then rinsed 3 times with autoclaved distilled water.

Floral tissues were discarded and floral axes were dissected into 2-3mm long pieces, without regard to nodal position. Each explant was placed in a vial (25×95mm) containing 10 ml

of modified MS medium with NAA and BA at 0.001g/L. each, 0.5g/L casein hydrolysate, and 30g/L sucrose, at a pH of 6.1 (Wright and Alderson 1980). After 0, 1, 2, 3, 4, 5, or 6 weeks at 20° or 24°C, vials were placed at 5°C in the dark for 2 weeks, then returned to the original temperature (20° or 24°C).

Bulb-like structures developed on 80-90% of the explants 13 weeks after the initiation of the cultures, regardless of timing of the 2 weeks at 5°C. These structures appeared to possess an organized epidermis over a solid matrix and developed tunics and roots, but were not symmetrically formed, complete bulbs (Figures. 2-4).

LeNard and Cohat (1968) observed that when organs in tulip bulbs were insufficiently differentiated at the beginning of the cold treatment, the elongation process was prevented but bulbing could take place. Alderson and Rice (1986) reported a small bulb-like swellings formed directly on explants of 'Merry Widow', without the development of a 'leaf', when cultures were incubated 6 weeks at 20°C prior to an 8-week cold treatment.

While we have not recovered fully-developed bulbs from *in vitro* culture of floral axes, the formation of bulb-scales, complete with roots and tunic, suggests that cold period after explanting, but before the appearance of organized structures, alters the developmental pathway taken by meristems forming in culture. Since bulb-like structures formed on explants placed in the cold immediately after explanting, the relatively warm storage of bulbs required for elongation of the floral axis may suffice as the first warm portion of the natural thermoperiod. Experiments are in progress to determine the optimum length of the cold pulse given after explanting and to discover factors important in the generation of more complete bulbs.

LITERATURE CITED

Alderson, P. and R. Rice 1986. Propagation of bulbs from floral stem tissue In: Plant tissue culture and its agricultural applications. (Withers and Alderson, eds.). Butterworths, London. p 91-97.

DeHertogh, A., L. Aung and M. Benschop. 1983. The tulip: botany, usage, growth, and development. **HortReviews** 5:45-125.

Eijk, J. van. 1989. Personal communication.

LeNard, M. and J. Cohat 1968. Influence des temperatures de conservation des bulbes sur l'elongation, la floraison et la bulbification de tulipe (*Tulipa gesneriana* L.). **Ann. Amelior.** Plantes.18:181-215.

LeNard, M., C. Ducommun, G. Weber, N. Dorion and C. Bigot 1987. Observations sur la multiplication *in vitro* de la tulipe (*Tulipa gesneriana* L.) a partir des hampes florales prelèvées chez des bulbes en cours de conservation. **Agronomie** 7:321-329.

Miller, V. and C. Gould 1967. Fungicidal and phytotoxic effects of certain mercurials used to control fusarium basal rot of *Tulipa* bulbs. **Phytopathology** 57:1202-1205.

Niimi, Y. 1978. Influence of low and high temperatures on the initiation and the development of bulb primordium in isolated tulip embryos. **Sci. Hort.** 9:61-69.

Nishiuchi, Y. 1979. Studies on vegetative propagation of tulip. II. Formation and development of adventitious buds in the excised bulb scale cultured *in vitro*. **J. Japan. Soc. Hort. Sci.** 48:99-105.

Nishiuchi, Y. 1980. Studies on vegetative propagation of tulips. IV. Regeneration of bulblets in bulb scale segments cultured *in vitro*. **J. Japan. Soc. Hort. Sci.** 49:235-240.

Rice, R., P. Alderson and N. Wright 1983. Induction of bulbing of tulip shoots *in vitro*. **Sci. Hort.** 20:377-390.

Taeb, A. and P. Alderson 1987. Micropropagation of tulip: Optimising shoot production from floral stem explants. **Acta Hort.** 212:677-681.

Wright, N. and P. Alderson 1980. The growth of tulip tissues *in vitro*. **Acta Hort.** 109:263-270.

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Environmental Requirements for Flowering and Bulb Growth in *Nerine sarniensis*

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SUMMARY

Bulbs of *Nerine sarniensis* 'Salmon Supreme' were grown at three temperatures (constant 14, 22 and 30 °C) and within each temperature at three photosynthetic photon fluxes (315, 450 and 695 μmol $m^{-2}s^{-1}$). A high proportion of bulbs (93 to 100% depending on PPF) flowered at 22 °C whereas only 33 to 35% flowered at 14 °C. Flowering was also more rapid at 22 ° C (90 days) than at 14 °C (128 days). A second inflorescence was produced from 42% of the bulbs grown at 22 °C, whereas, none were produced from bulbs grown at 14 °C. Flower quality attributes, including scape length and diameter and flower fresh-weight, were also superior at 22 °C, but bulb dry-weight accumulation and off-set production were highest at 14 °C. Bulbs grown at 30 °C remained semi-dormant for 129 days after which they were transferred to 22 °C where growth commenced. Subsequent flower production and vegetative growth following transfer was inferior to that of bulbs maintained throughout at 22 °C. Low PPF enhanced flower stem (scape) length and leaf area expansion but reduced bulb dry-weight by 20 to 30%.

INTRODUCTION

The genus *Nerine* is made up of approximately 30 species of flowering bulbs (Norris 1974) belonging to the Amaryllidaceae family. It is closely allied to genera such as *Amaryllis* and *Vallota*. Nerines have a very simple growth form; bulbs produce strap-shaped leaves and an inflorescence comprising a naked flower stem that supports an umbel of six-petalled florets. The petals are usually recurved and can also be waved or crimped. The range of floret colors includes red, pink, orange, salmon, bronze, mauve and white, and these occur in many shades and tones. Florets are outstanding for their clarity of color.

All species of *Nerine* are native to South Africa. In northern regions, where the predominant period of rainfall occurs in summer months, the foliage of the indigenous species emerges in summer and the bulbs are dormant in winter. In these species, such as *Nerine bowdeni*, *N. undulata* and *N. angustifolia*, the flower (inflorescence) emerges at the end of the vegeta-

tive growth period. The species of *Nerine* indigenous to southern regions (winter rainfall) have foliage that emerges in the autumn and the bulbs are summer dormant. In species that are dormant during the summer, such as *N. sarniensis, N. curvifolia, N. pudica* and *N. humilis*, the flowers emerge before significant leaf expansion has occurred. Species which occur between the two geographical extremes, such as *N. flexuosa*, have foliage which appears in flushes year-round, there is no distinct rest period, and flowering can occur at any time.

Nerine sarniensis grows naturally on mountain slopes above 300m in the mountains of the extreme South-West Cape, including Table Mountain. It is frequently known as the Guernsey lily. In Europe, it is grown as a greenhouse crop because of the need to provide warm conditions during the main growth period from autumn to spring. In New Zealand, however, where winters are mild in the oceanic climate, it appears that commercial crops can be grown outdoors if some protection from wind and rain is provided to ensure the production of high-quality cut-flowers and so that cold temperatures below 5°C are avoided.

The environmental requirements for flower production and bulb growth in *N. sarniensis* are largely unknown. In contrast, there is a considerable understanding of the environmental physiology of *N. bowdeni* (e.g. Berghoef and van Brenk 1983; Sytsema 1971, 1975). Information about the influence of temperatures on flower production, leaf development and bulb growth in *N. sarniensis* is essential for the optimum management of greenhouse conditions and for the selection of appropriate out-door sites for either commercial cut-flower or bulb production. Equally, because shading is often used in horticultural production systems to reduce temperature, an understanding of the influence of light intensity is also important.

In addition to the commercial importance of the species *N. sarniensis*, and its forms such as 'Corusca' and 'Fothergillii', it is extensively used as the primary parent in breeding programmes. An understanding of the influence of environment on the species is, therefore, also likely to add to our knowledge of the performance of those hybrids arising from breeding programs where *N. sarniensis* is used as a parent.

The objectives of this research were to study the influence of both temperature and light intensity on flower production, flower quality and bulb growth. As little is known about the environmental requirements of this species, the treatments used were chosen to cover a broad range of conditions so that the general growth and development responses to these two environmental factors could be identified.

MATERIALS AND METHODS

Dormant bulbs of *N. sarniensis* 'Salmon Supreme' were lifted from the field in late January (i.e mid-summer), and cool-stored at 4°C for 90 days, and then planted into 1.2L capacity pots (one bulb per pot) containing peat:pumice (5:3 v/v) growing medium. Each pot was supplied with 100ml of complete nutrient solution (half-strength Hoagland's A) three times daily via microtubes from an automated watering system.

The temperature and photosynthetic photon flux (PPF) treatments were imposed in each of three walk-in controlled environment rooms at the DSIR Climate Laboratory in Palmerston North, New Zealand. The three temperature treatments were constant 30, 22 and 14±0.5°C. A constant vapour pressure deficit of 0.4kPa was used which resulted in respective relative humidities of 90, 83 and 72±5%. The day length was 12 hours. Low PPF treatments within each room were achieved by covering individual trolleys with spectrally-neutral shade cloth. The resultant mean PPF values obtained were 695, 450 (35% shade) and 315 (55% shade) μmol $m^{-2}s^{-1}$. These PPF treatments were randomly arranged within each controlled environment room.

There were 15 bulbs in each temperature×PPF treatment and these were arranged as two blocks, of 7 and 8 bulbs, on separate trolleys. Bulbs were maintained in the 14 and 22 °C treatments for 185 days when half were dissected and vacuum dried for dry-matter assessment. Bulbs were grown in the 30 °C treatment for 129 days (where they failed to actively grow) after which they were transferred to the 22 °C treatment for a further 56 days before harvest.

During growth, the times of flower bud appearance and opening of the first floret were recorded for each developing inflorescence. At anthesis, flower quality was assessed by recording flower stem (scape) length, stem diameter, floret number and the fresh-weight of the inflorescence.

At the conclusion of the experiment, the numbers of flower primordia and developing leaves were recorded in the dissected bulbs. During harvest, off-set number, bulb diameter, root, bulb and leaf dry-weight, and the area of expanded leaves on both the original bulb and the off-sets were recorded.

RESULTS

The best flowering performance occurred under the 22 °C conditions where 95% of the bulbs produced a flower 90 (SEM±4) days after the start of the treatments (Table 1) and a second flower was produced from 42% of the bulbs 37 days after the first flower appeared. In contrast, only 35% of the bulbs in the 14 °C treatment produced a flower and no bulbs produced two flowers; the mean day number for first flower appearance was 124 (SEM±15).

The most dramatic response observed in the treatments was the failure of the bulbs in the 30 °C conditions to produce any significant growth. Root growth from these bulbs was poor, only very limited leaf growth took place, and no flowers emerged while the bulbs remained in that treatment. A high proportion of bulbs (73%) from the 30 °C treatment flowered after they were transferred to the 22 °C conditions. Scape elongation was rapid and floret opening occurred 10 days after transfer. However, in contrast to the bulbs maintained throughout the experiment at 22 °C, only 8% of those transferred from 30 to 22 °C produced a second flower within the 56 day treatment period at 22°.

The quality of the inflorescence was superior in the 22° C treatments where flower stem length was greater than at either 14 or 30 °C and stem diameter and flower fresh-weight were higher ($P<0.01$) than at 30 °C (Table 1). Floret number did not appear to be affected by temperature.

At 22 °C the quality of the second flower produced was, apart from a small reduction in fresh-weight, almost identical to that of the first flower. This was in contrast to the bulbs grown initially at 30 °C. Prolonged exposure to the high temperature conditions resulted in a decrease in the stem diameter of the second flower (5.7cf. 4.6mm; $P<0.01$), in flower fresh-weight (12.4cf. 9.3g; $P<0.07$) and floret number (9.4cf. 5.8; $P<0.05$) but not of stem length (34.0cf. 39.7cm).

In all of the temperature treatments, PPF had no consistent influence on the proportion of bulbs that flowered or on the rate of flower development. Although a reduction in PPF from 695 to 315 μmol $m^{-2}s^{-1}$, resulted in an increase ($P<0.08$) in stem length, shading had no influence on flower stem diameter, number of florets per inflorescence or flower fresh-weight (Table 1).

The vegetative development of the bulbs was markedly affected by temperature. At 22 °C, leaf number was one-third higher than at 14 °C and leaf area was two to three times greater (Table 2). After 185 days, the diameter of bulbs was similar in both the 14 and 22 °C treatments, but bulb dry-weight was greater ($P<0.01$) under the cooler temperature conditions, presumably indicating greater accumulation of reserves in the leaf bases. Bulbs from the

original 30°C conditions had considerably reduced leaf number, leaf area, bulb diameter and dry-weight values at the end of the study compared with values from other temperature treatments.

The main consequence of a reduction in PPF on vegetative growth was to increase both leaf area and leaf dry-weight, although differences were not significant ($P < 0.05$) for either character between the two low PPF treatments (Table 2). Other vegetative growth characters were not affected by PPF except at 14°C where both total plant and bulb dry-weights were smaller ($P < 0.05$) when plants were grown at 315 μmol $m^{-2}s^{-1}$ than at the higher PPF's.

The proportion of bulbs that produced off-sets was highest at 14°C (95%) compared with 77 and 74% at 22 and 30°C, respectively (Table 1). There was a higher number of off-sets per bulb at 22 than at 30°C ($P < 0.05$) but the numbers were similar at 14 and 22°C. At 30°C, the total dry-weight of off-sets per bulb (0.85g) was lower ($P < 0.05$) than at either 14 or 22°C (2.1 and 2.6g, respectively).

The dissections carried out at the end of the study provided some information about the vegetative and floral development that had occurred in the bulbs during each of the treatments. In addition to the flowers that emerged and were harvested, at 14 and 30°C two flower buds and at 22°C three flower buds were present in bulbs at the end of the treatment period. The higher number at 22°C was presumably a consequence of more rapid development as evidenced by the higher number of expanded leaves in that treatment. It was also evident that a large proportion of the unemerged flower buds had aborted in the outer bulb positions (i.e., the most developed buds) under all PPF conditions in the 14°C temperature. In contrast, only a small proportion of the flower buds at both 22 and 30°C aborted. Although there was some variability, on average 7 leaves (including scale leaves) were produced between successive flower bud primordia.

DISCUSSION

Observations of the flowering behaviour of *N. sarniensis* in the wild indicate that less than half of the bulbs in a given area flower in any particular season (Norris 1974). In greenhouse research, van Brenk (1984) achieved only 60% flowering in *N. sarniensis* 'Corusca Major' and breeders of this species (e.g. Norris 1974; Smithers 1984) have similarly recorded that flowering is often poor in their populations. The achievement of a high proportion of flowering in bulbs is possible, however, as evidenced by the 93-100% level reached in our study under the constant 22°C growing conditions.

Aside from the differences in the proportion of bulbs that flowered, the 22°C temperature that resulted in the maximum proportion of bulbs flowering in our study is close to the 17 and 21°C conditions found to produce maximum flowering by van Brenk (1984). At 9, 13 and 25°C he achieved only 25 to 35% flowering which is consistent with our results obtained at both 14 and 30°C.

The lack of significant growth while the bulbs were at 30°C in our study, and at 25°C in van Brenk's, is consistent with the summer-dormant growth habit of this species. Temperature (presumably as well as rainfall distribution and frequency) appears, therefore, to have a major impact on the growth cycle of the crop. In greenhouse and field sites, sustained periods of temperature above about 25°C should be avoided during the late summer-autumn period if flowering is required at that time, otherwise it will be delayed until early winter when temperatures decline naturally. The results also indicate that flower quality will be reduced under sustained high temperature conditions.

Equally, low temperatures should be avoided early in the growing season if a high proportion of flowering bulbs is to be achieved and if flower development and scape elongation are to proceed at an acceptable rate. The difference in temperature from 22 to 14 °C reduced flowering from 95 to 35% and extended the time to flower harvest by 34 days, by which time almost half of the bulbs at 22 °C had produced a second flower. Flower stem length was also longer at 22 °C. Maintaining mean temperatures above 14 °C during the flower production season is, therefore important if good yields of high quality flowers are to be realised.

The dissection data showed that the indication of new flower buds continued under all of the temperature regimes studied. The reason for a reduction in the proportion of bulbs that flowered, at both high and low temperatures, was primarily due to abortion occurring on flower buds that were developing but had not emerged from the bulb. Each flower bud was formed in succession after a cycle of 7 leaves (including scale leaves) had been produced in the bulbs studied.

In contrast to the requirements for warm temperatures early in the season for superior flower development, it appears that cooler temperatures close to 14 °C lead to heavier bulbs and greater off-set production. With field-grown material the natural seasonal progression will lead to a decline in temperatures following flowering. In greenhouse-grown crops, once flowering is finished, lower heating and ventilation set-points could be used to enhance bulb growth and therefore reduce energy consumption.

The responses of both flowering and vegetative growth to the temperature regimes used in this study are in close agreement with the cycle and range of temperatures experienced in the natural centre of origin of the species. The long-term meteorological records from Cape Town give a general indication of the temperatures experienced in the South-West Cape and Table Mountain regions (Anon. 1983). Although environment will vary from one microsite to another, mean temperatures in the February-March-April period (flowering occurs naturally in mid-March) are in the 18 to 22 °C range whereas later in winter, when vegetative growth is occurring, they are in the 13 to 15 °C range (Table 3).

While light intensity did not produce dramatic differences in floral or vegetative growth responses, it is clear that shade typical of that used in this study could be tolerated during flowering with some increase in stem length occurring without any loss of other flower quality attributes. However, the results do strongly indicate that shading subsequent to flowering during the main vegetative bulb growth phase should be avoided—both total plant and bulb dry-weights were 20 to 30% lower than unshaded values at both 14 and 22 °C where 55% shading had been used.

LITERATURE CITED

Anon. 1983. Official Yearbook of the Republic of South Africa. 9th Edition. Cr. V. Rensburg Publications.

Berghoef, J. and G. van Brenk 1983. Effect of temperature on flowering of *Nerine bowdeni* W. Watts. **Acta Hort.** 134: 41-48

Brenk, G. van 1984. Invloed bewaaromstandigheden en de teelttemperatuur op de groei en bloei van *Nerine sarniensis* 'Corusca Major' (Influence of storage conditions and growth temperature on the growth and flowering of *Nerine sarniensis* 'Corusca Major'). Unpublished report (Trial 92/32,). Vakgroep Tuinbouwplantenteelt, Landbouwhogeschool, Wageningen.

Norris, C.A. 1974. The genus of *Nerine*, part II. **The Nerine Society Bulletin** (ed. C.A. Norris), No. 6

Smithers, P. 1984. The enigma of hybrid nerines. **Herbertia** 40: 82-93.

Sytsema, W. 1971. Effects of storage and date of planting on flowering and bulb growth of *N. bowdeni*. **Acta Hort.** 23: 99-105.

Sytsema, W. 1975. Flowering and bulb growth of *N. bowdeni*. **Acta Hort.** 47: 241-249.

Table 1. Flowering & flower quality characteristics of *N. sarniensis* 'Salmon Supreme' growing at different temperature and PPF conditions (± standard error of mean).[z]

	Temperature (±0.5 °C)								
	14			22			30[y]		
	Photosynthetic photon flux (μmol $m^{-2}s^{-1}$)								
	315	450	695	315	450	695	315	450	695
Proportion of bulbs producing 1 inflorescence (%)	33	36	36	93	93	100	85	54	79
Proportion of bulbs producing 2 inflorescences (%)	0	0	0	40	21	64	0	8	17
Time to first flower (days)	121 (28)	161 (10)	103 (25)	91 (10)	95 (7)	84 (6)	139 (4)	144 (5)	135 (2)
Stem (scape) length (cm)	38 (2)	35 (1)	32 (2)	45 (1)	44 (1)	36 (2)	37 (1)	35 (2)	30 (3)
Stem (scape) diameter (mm)	6.3 (0.4)	6.5 (0.2)	5.5 (0.5)	6.3 (0.2)	5.9 (0.2)	6.2 (0.2)	5.6 (0.2)	5.5 (0.2)	5.9 (0.2)
Number of florets	9.0 (1.4)	10.9 (0.5)	9.8 (1.3)	8.9 (0.6)	8.8 (0.5)	9.9 (0.6)	9.7 (1.1)	8.4 (1.1)	9.7 (0.8)
Flower fresh-weight (g)	17.0 (3.1)	16.3 (0.9)	15.3 (2.6)	20.0 (1.4)~	15.6 (0.9)	15.6 (1.8)	13.2 (0.8)	11.4 (0.6)	12.4 (1.1)

[y]Bulbs transferred to 22 °C on day 129.

Table 3. Average daily maximum (^{T}max), minimum (^{T}min) and mean temperatures (°C), and average monthly rainfall (mm) for Cape Town (20 year mean).

Month	^{T}max (°C)[z]	^{T}min (°C)	^{T}mean (°C)	Rainfall (mm)
Jan.	26	16	21	17
Feb.	27	16	22	15
March	26	15	21	22
April	23	13	18	49
May	20	10	15	94
June	19	9	14	109
July	17	8	13	94
August	18	9	14	83
Sept.	19	10	15	58
Oct.	22	12	17	40
Nov.	24	14	19	26
Dec.	26	13	20	20

[z]10 °C = 50 °F, 15 °C = 59 °F, 20 °C = 68 °F, 25 °C = 77 °F.

Table 2. Vegetative growth characteristics of *N. sarniensis* ('Salmon Supreme') growing at different temperature and PFD conditions (values ± standard error of mean).[7]

	Temperature (±0.5 °C)								
	14			22			30		
	Photosynthetic photon flux (μmol $m^{-2}s^{-1}$)								
	315	450	695	315	450	695	315	450	695
Leaf number	7.8 (0.5)	7.4 (0.6)	7.0 (0.5)	10.8 (0.4)	10.6 (0.7)	9.4 (0.9)	6.3 (0.3)	6.9 (0.5)	6.3 (0.3)
Leaf area (cm^2)	266 (14)	220 (32)	154 (17)	609 (36)	598 (51)	308 (54)	176 (17)	181 (23)	149 (18)
Leaf dry-weight (g)	1.90 (0.11)	1.37 (0.22)	1.30 (0.16)	5.01 (0.32)	5.03 (0.38)	3.18 (0.63)	1.10 (0.10)	1.19 (0.15)	1.14 (0.12)
Root dry-weight (g)	1.23 (0.24)	1.41 (0.10)	1.75 (0.20)	1.55 (0.14)	1.94 (0.31)	0.94 (0.38)	0.37 (0.04)	0.43 (0.07)	0.53 (0.05)
Bulb dry-weight (g)	7.96 (0.36)	10.93 (0.84)	11.33 (0.80)	5.53 (0.64)	8.85 (1.00)	7.23 (1.25)	3.71 (0.41)	4.11 (0.55)	4.51 (0.38)
Total plant dry weight (g)	11.17 (0.64)	13.71 (0.85)	14.38 (1.08)	12.09 (0.88)	15.81 (1.16)	11.35 (2.19)	5.18 (0.42)	5.73	6.19
Bulb diameter (mm)	41.1 (0.6)	44.7 (1.4)	44.6 (1.6)	43.4 (1.5)	48.3 (1.5)	42.8 (4.1)	35.4 (2.2)	39.8 (2.9)	38.5 (2.0)
Off-set number/bulb	2.0 (0.5)	2.4 (0.8)	2.1 (0.5)	1.8 (0.6)	2.3 (0.8)	1.9 (0.5)	1.0 (0.2)	0.9 (0.3)	1.4 (0.3)
Propn. bulbs with off-sets (%)	100	86	100	75	71	86	78	63	80

[7]Off-set data excluded from all leaf, root and bulb values.

ADAPTATION OF 'SANS SOUCI' LILIES TO POTTED PLANT CULTURE

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ABSTRACT

LILIUM 'Sans Souci' is usually grown as a cut flower, but would be a good new potted plant for American markets if height could be effectively controlled. We conducted two experiments to determine the effectiveness of ancymidol and XE-1019 in reducing height when applied as a foliar spray, soil drench, bulb dip, chemigation, or combinations of these. In Experiment 1 XE-1019 applied as a spray at 1 to 25ppm was as effective in reducing stem length as a drench at 0.1 to 0.5mg ai/plant. Ancymidol applied as a foliar spray at 66 and 132ppm was as effective as a drench at 0.25mg ai/plant. In experiment 2 plants sprayed with ancymidol at 0.25mg ai/plant were 6% shorter and at 0.5mg ai/plant were 12% shorter than untreated plants. Similarly where plants were drenched with ancymidol at 0.25mg ai/plant, height was reduced by 9%. The height reduction of plants where the bulbs had been dipped in 100 ppm ancymidol was 21% compared to untreated plants. Plants were 22% shorter than controls when ancymidol was applied through the irrigation water (chemigation). The effectiveness of ancymidol and XE-1019 in reducing stem length depended on the method of application. Ancymidol was most effectively applied as a bulb dip or chemigation and XE-1019 was equally as effective applied as a spray or drench. Combining the bulb dip with either a spray or drench was more effective than either treatment individually.

INTRODUCTION

Hybrid lilies are usually grown as cut flowers, but there is increased demand for them as potted flowering plants (Corr *et al.* 1985). The major problem with most hybrid lilies, like the oriental cultivar 'Sans Souci', is that they are too tall.

The objective of the research was to determine which growth retardants and at what rates would reduce the height of 'Sans Souci' enough to permit the use of it as a flowering potted plant.

MATERIAL AND METHODS

EXPERIMENT 1

On 20 January 1987, commercially case-cooled bulbs of 'Sans Souci' were potted one per pot in a 16cm pot using a peat-like mix. Bulbs were forced in a greenhouse where the night temperature was set at 16°C and ventilation set at 21°C. The plants were irrigated as needed with a fertilizer solution made from 16-4-12 at 1.5g/L. XE-1019 was applied as a spray at 0, 1, 3, 5, 10 and 25 ppm and ancymidol at 66 and 132 ppm. XE-1019 was applied as a soil drench at 0, 0.1, 0.3, and 0.5mg per plant, and ancymidol at 0.25 and 0.5mg per plant. For the spray treatments about 5ml of solution was applied per plant, while as a drench 100ml were applied to each pot. A completely randomized design was used with 7 plants per treatment.

Plants were drenched on 20 February and sprayed on 23 February 1987. The data collected at the end of the experiment were date of anthesis, number of flowers and length of the stem.

Experiment 2

Uncooled bulbs of 'Sans Souci' were received 28 October 1987, case cooled at 4 °C until 9 December then at 2 °C until 6 January 1988. The bulbs were potted in a peatlite growing mix, and they were moved to a greenhouse set at 17 °C at night and ventilated at 24 °C. Ancymidol and XE-1019 were applied as a bulb dip, growing mix drench, foliar spray or metered into the irrigation water daily (chemigation). The foliar sprays were applied when the plants were either 7-8cm or 14-16cm tall. The specific rates are listed in Table 1. In addition to the individual treatments bulbs dips were combined with either a drench or spray application. For the combination the drench was applied at emergence and the spray was applied at 7-8cm. The plants were irrigated as needed with a fertilizer solution made from 16-4-12 at 1.5g/L. Chemigation treatment plants were irrigated each day with a solution containing the growth retardant plus the same fertilizer and rate as used on the rest of the plants. The design was a randomized complete block design with 4 blocks and 3 plants per block.

As each plant flowered we recorded the days to flowering, stem length and the number of flower buds.

RESULTS

Experiment 1

A 1 ppm XE-1019 spray reduced stem length by 24%, while a 25 ppm spray reduced stem length by 38% compared to the control (Figure 1). Ancymidol at 66 ppm restricted height by 20%, and at 132 ppm by 28%. The drench and spray methods of application were equally effective for both XE-1019 and ancymidol treatments. There was no effect of the growth retardants on the number of flowers per plant (Table 2). The number of days from planting until flowering was affected by the growth retardants (Table 2). In general the plants drenched either ancymidol or XE-1019 were delayed in flowering compared to the sprayed plants except for the 25 ppm XE-1019 spray. The increased crop time due to the growth retardants was generally less than a week and should not create problems for the grower. The appearance of the plant was changed by the retardant treatments. The treated plants appeared more compact with closely spaced leaves than the controlled plants.

Experiment 2

Ancymidol as a bulb dip reduced the stem length of 'Sans Souci' compared to the control (Figure 2). The largest difference in height was between the control and the 50 ppm dip. There was additional reduction in stem length as the concentration of the dip increased. The ancymidol spray at 14-16cm produced plants slightly shorter than when applied at 7-8cm. There was no difference in effect on stem length whether ancymidol was applied as a spray at 50 ppm or 200 ppm. The ancymidol spray produced slightly shorter plants than any of the drenched treatments. Height of plants drenched at emergence or 7-8cm were equal. No difference was recorded in height of plants treated with 0.25 or 0.5mg of ancymidol. The chemigation method of application of ancymidol was effective in reducing stem length. The 0.02mg rate produced more retardation than the 0.01mg rate. No consistent effect of ancymidol on flower number or days to flowering was observed (Table 3).

Table 1. Growth retardant rates for Expt. 2.

Ancymidol

Dip rates

1. 0 ppm (Control)
2. 50 ppm
3. 100 ppm
4. 200 ppm

Spray rates (Applied about 2.5 ml of solution per plant.)

1. 0 ppm (Control)
2. 50 ppm (0.12 mg/pot)
3. 100 ppm (0.25 mg/pot)
4. 200 ppm (0.50 mg/pot)

Timing of Sprays (Sprays were applied)

1. When stem length is 7-8 cm (about 3 in.)
2. When stem length is 14-16 cm (about 6 in.)

Drench treatments (These were applied at emergency.)

1. 0.00 mg/pot
2. 0.01 mg/pot
3. 0.50 mg/pot

Chemigation treatments (These were applied after potting.)

1. 0.00 mg/day in the irrigation water
2. 0.01 mg/day in the irrigation water
3. 0.02 mg/day in the irrigation water

XE-1019

Dip rates

1. 0 ppm (Control)
2. 5 ppm
3. 10 ppm
4. 20 ppm

Spray rates (Applied about 6 ml of solution per plant.)

1. 0 ppm (Control)
2. 1 ppm (0.005 mg/pot)
3. 2 ppm (0.010 mg/pot)
4. 5 ppm (0.025 mg/pot)

Timing of Sprays (Sprays were applied.)

1. When stem length is 7-8 cm (about 3 in).
2. When stem length is 14-16 cm (about 6 in).

Drench treatments (These were applied at emergence.)

1. 0.00 mg/pot
2. 0.25 mg/pot
3. 0.50 mg/pot

Chemigation treatments (These were applied after potting.)

1. 0.00 mg/day in the irrigation water.
2. 0.01 mg/day in the irrigation water.
3. 0.02 mg/day in the irrigation water.

Table 2. Effect of XE-1019 and ancymidol as a spray and drench on 'Sans Souci' Lilies (Experiment 1).

TREATMENTS	FLOWERING DATE	DAYS TO FLOWERING	# OF FLOWERS
Spray			
XE-1017			
0 ppm	4/20	59.7 h[z]	7.2
1 ppm	4/22	1.5 efgh	6.8
3 ppm	4/22	61.0 gh	5.8
5 ppm	4/21	60.0 h	5.8
10 ppm	4/22	61.3 fgh	6.3
25 ppm	4/26	65.3 abc	6.7
Ancymidol			
66 ppm	4/23	62.2 defgh	6.0
132 ppm	4.22	60.8 h	6.3
Drench			
XE-1019			
0	4/25	64.3 bck	5.4
0.1 mg	4/25	64.1 bcde	6.2
0.3 mg	4/25	63.6 cdefg	6.9
0.5 mg	4/28	66.8 ab	7.0
Ancymidol			
.25 mg	4/25	63.9 cdef	6.7
.5 mg	4/26	64.7 abcd	5.8
Significance		*	NS

[z] Means separation by Duncan-Waller at the 5% level.

Dipping, spraying or drenching with XE-1019 restricted height of 'Sans Souci' (Figure 3). A 5 ppm dip reduced height compared to the control, but the 10 ppm dip was about the same as the 5 ppm dip. The 20 ppm dip produced shorter plants than did the 5 to 10 ppm. There was little difference in effect when the spray of XE-1019 was applied at 7-8cm or at 14-16cm tall. The 1 ppm spray produced plants that were shorter than the control plants, and those treated with 2 ppm were shorter than with 1 ppm; however, those treated with 5 ppm were similar to those sprayed with 2 ppm. An XE-1029 was not as effective as the spray treatments, but as effective as the drench treatment. The number of flowers per plant was not affected by any XE-1019 treatment (Table 3). There was quite a bit of variability in days to flowering thus no trends are evident.

Combining an ancymidol bulb dip with a drench reduced height more than either alone (Figure 4). The combination of the bulb dip with the spray also reduced the height more than a single application (Figure 4). It appears that the effects are additive.

Combining an XE-1019 bulb dip with a drench reduced height more than either one alone (Figure 5). The combination of the bulb dip with the spray also reduced the height more than a single application (Figure 5). It appears that the effects are additive.

DISCUSSION

Dicks and Rees (1973) reported that two mid-century hybrid lily cultivars drenched with ancymidol at 0.5mg/plant were shorter than those drenched at 0.25mg. In contrast we found

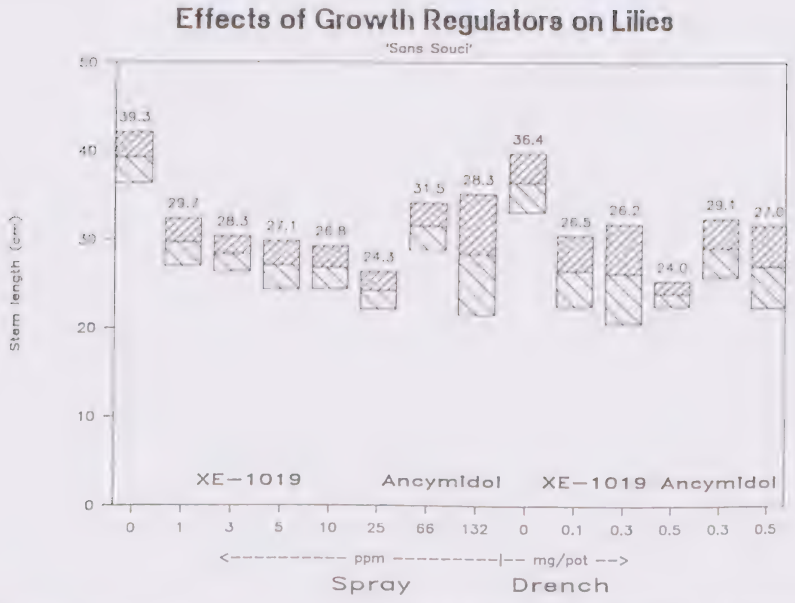

Figure 1. Effect of XE-1019 and ancymidol on the stem length of 'Sans Souci' Lily (Experiment 1). The cross hatched area represents plus and minus a standard error of the mean.

Table 3. Effect of ancymidol and XE-1019 on number of flowers, and days to flower of 'Sans Souci' lily (Experiment 2).

	ANCYMIDOL		XE-1019	
Flowers	No. of Flowers	Days to Flower	No. of Flowers	Days to Flower
Control	6.1	128	5.4	121
Dip 50	5.1	124	5.8	129
Dip 100	5.2	130	6.4	124
Dip 200	5.8	134	6.3	130
Spray 50 7-8 cm	5.8	130	5.0	121
Spray 100 7-8 cm	5.8	130	5.5	128
Spray 200 7-8 cm	6.4	130	5.4	132
Spray 50 14-16 cm	6.0	125	5.8	122
Spray 100 14-16 cm	5.3	128	5.5	132
Spray 200 14-16 cm	6.5	125	5.3	132
Drench 0.25 Emer.	5.7	121	5.7	124
Drench 0.5 Emer.	6.4	126	5.3	128
Drench 0.25 7-8 cm	5.9	124	6.0	124
Drench 0.5 7-8 cm	5.5	126	5.8	126
Chemigation 0.01	6.1	121	5.3	126
Chemigation 0.02	5.8	125	5.2	126

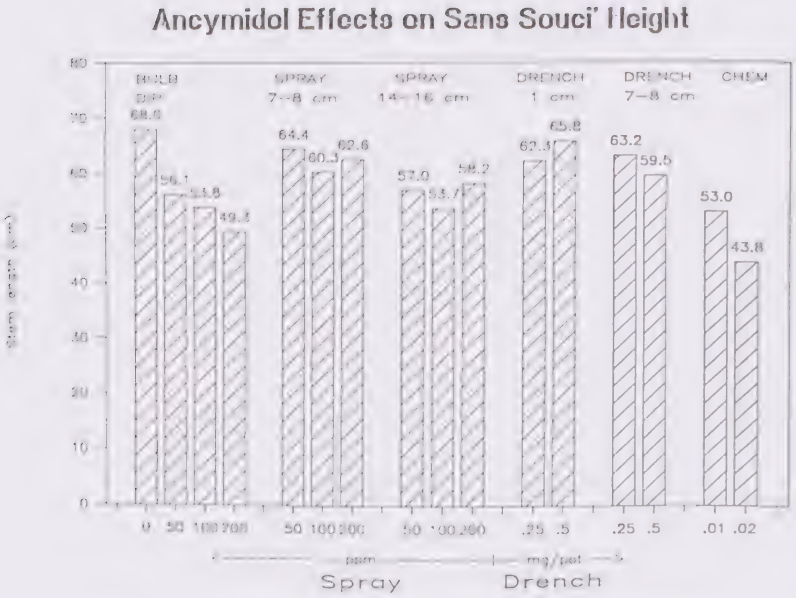

Figure 2. Effect of ancymidal on stem length of 'Sans Souci' lily (Experiment 2).

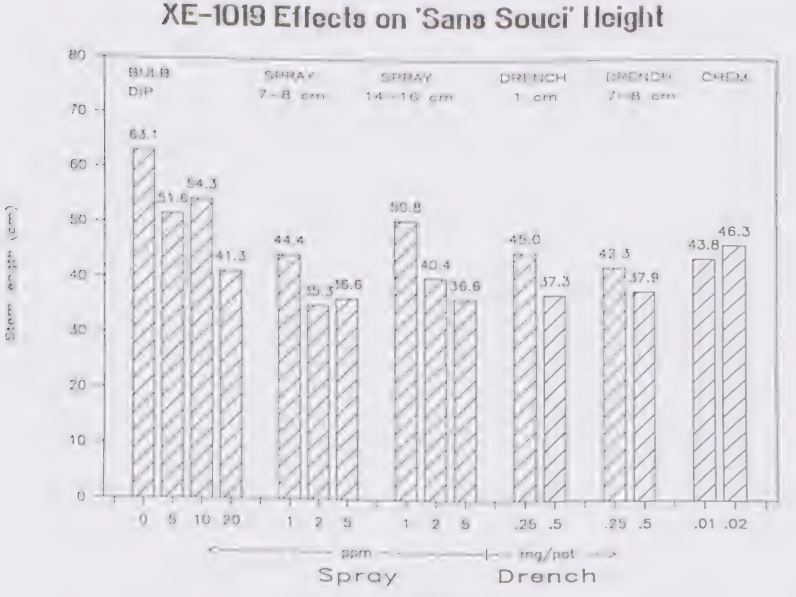

Figure 3. Effect of XE-1019 on stem length of 'Sans Souci' lily (Experiment 2).

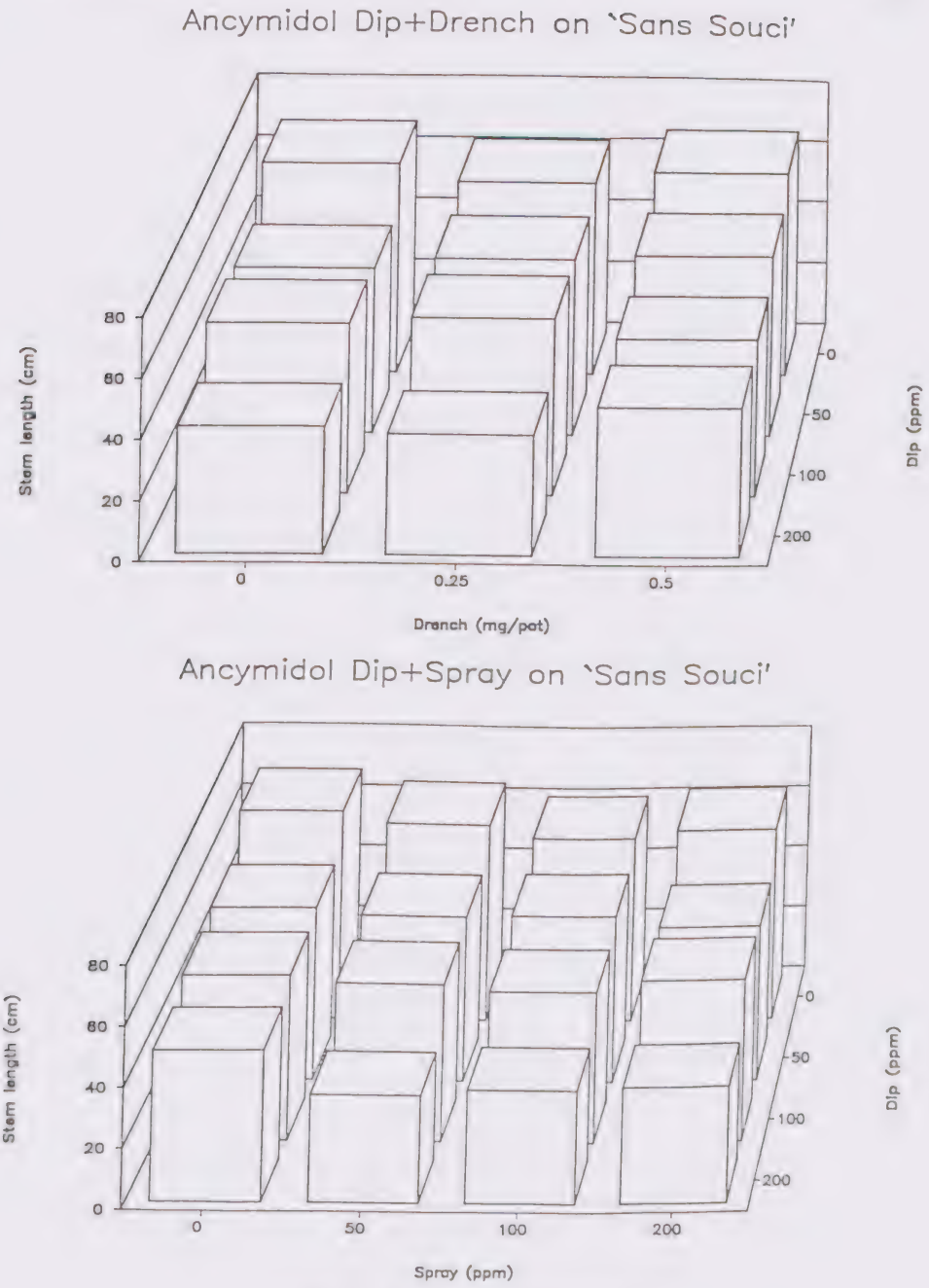

Figure 4. Effect of an ancymidal bulb dip corm.

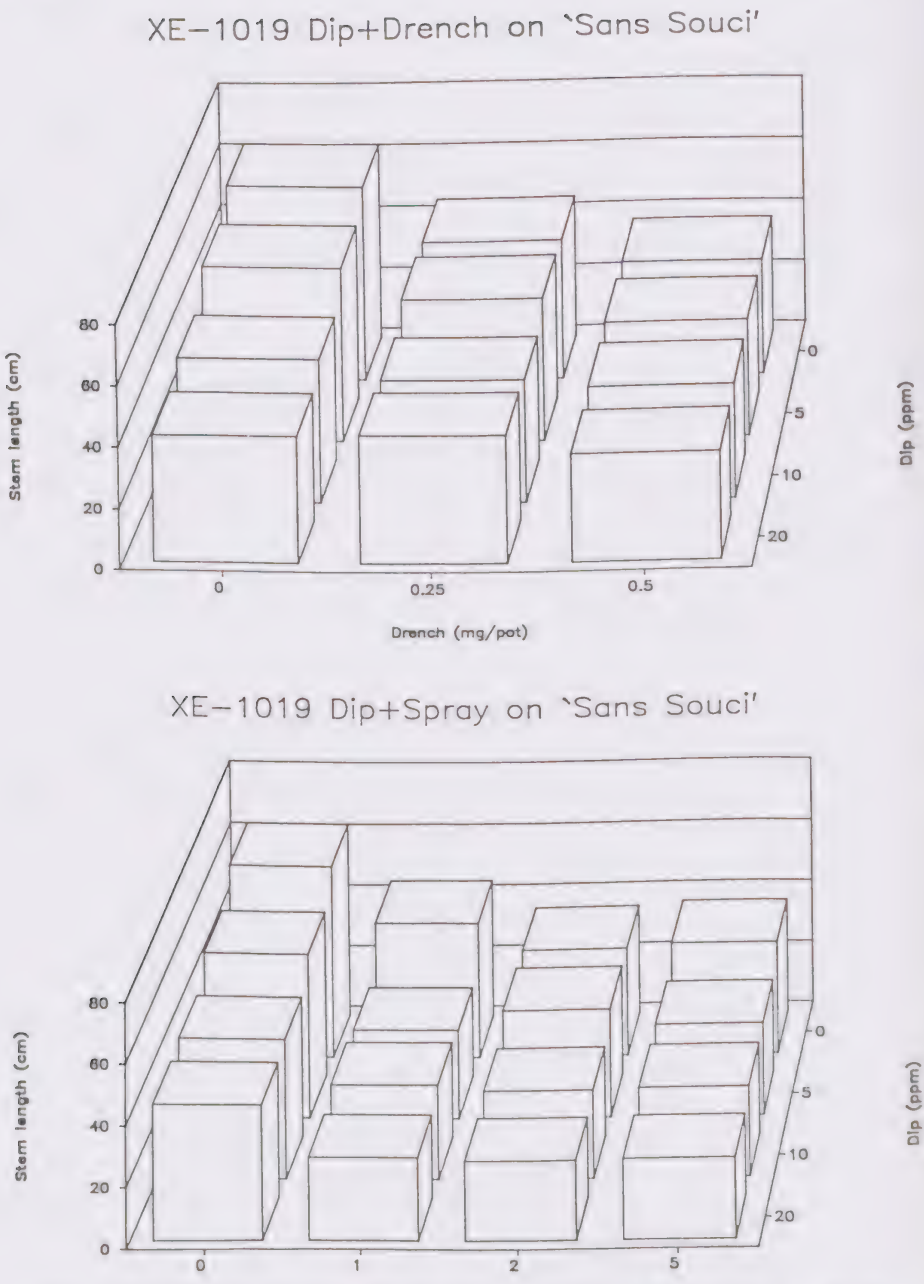

Figure 5. Effect of an XE-1019 bulb dip combined with either XE-1019 drench or spray on stem length of 'Sans Souci' lily (Experiment 2).

there was no height difference between plants treated with 0.25mg and those treated with 0.5mg of ancymidol.

White (1976) reported that an ancymidol drench at emergence was less effective than a drench applied at a height of 3.6cm. Here an ancymidol drench at emergence was as effective as one applied at 7.6cm. Wilfret (1987) determined that XE-1019 was effective as a drench on Easter lilies. In this work XE-1019 was found to be effective as a soil drench on 'Sans Souci'.

Wilfret (1987) also reported that for Easter lily ancymidol sprays and drenches were equally effective. We found the spray was slightly more effective than the soil drench. Wilfret (1987) reported that when the spray ran down the stem of a lily and was absorbed by the soil, the height was restricted more than with a drench application alone. It is possible that some of the ancymidol spray entered the medium and was taken up into the plant. For XE-1019 Wilfret (1987) reported the spray to be more effective than the drench, which agrees with the results obtained in this experiment. It is not clear why there was little effect of rate of ancymidol spray on stem length in this experiment. XE-1019 as a spray did restrict stem length more than at higher rates.

Simmonds and Cumming (1977) reported that more dwarfing of the stem was obtained by using a 12 hour bulb dip than a soil drench. Lewis and Lewis (1981) reported that a 2 sec. dip was effective for Easter lilies. Lewis and Gilbertz (1987) reported that an ancymidol dip was effective in restricting height of 'Gold Nugget' hybrid lily. This experiment demonstrated that ancymidol as a dip was effective for the oriental hybrid lily 'Sans Souci'. This experiment also demonstrated that XE-1019 can be effectively used as a bulb dip.

White (1976), working with mid-century hybrid lilies, reported that the days to flowering and the number of flower buds were not affected by ancymidol. Similarly, we report here that number of buds and the days to flowering were not affected in 'Sans Souci'.

Holcomb and White (1970) reported that applying CCC in the irrigation water (chemigation) was not as effective at controlling height of poinsettias as a single drench. In this experiment with ancymidol the chemigation was superior to a single drench, while with XE-1019 the drench was superior to the chemigation.

Little work has been reported combining bulb dips with either a spray or drench. An example for ancymidol would be a 200 ppm dip produced a 28% reduction in stem length compared to the control. A 200 ppm spray gave a 9% reduction while a combination of 200 ppm spray plus a 200 ppm dip gave a 44% reduction in height. A possible explanation would be that more active ingredient was taken up thus the retardation was greater. With XE-1019 the effects were slightly different. The 20 ppm dip gave a 35% reduction in height and the 2 ppm spray gave a 43% reduction in height while the combination gave a 59% reduction in stem length. In this case it would seem that we may be near the maximum reduction possible thus the additional XE-1019 is not having equal effect.

A loss of lower leaves was observed in 'Sans Souci' and may have been related to the amount of growth retardant. The more retardant applied, the more the lower leaf loss. When the plants were short enough to be acceptable as a potted plant, the lower part of the stem was bare which detracted from the aesthetics of the plant.

CONCLUSIONS

The height of 'Sans Souci' was reduced by both ancymidol and XE-1019. Spray and drenches of both retardants were equally effective in controlling height in 'Sans Souci'. Chemigation was more effective than spraying or drenching ancymidol but spraying and drenching was more effective with XE-1019.

The ancymidol rates we use seemed to be too low to provide an optimum height potted plant. XE-1019 did provide adequate height control so that plants were acceptable as potted plants. XE-1019 as a bulb dip at 20 ppm or a spray at 2 or 6 ppm or a drench at 0.5mg ai/plant all provided adequate height control.

LITERATURE CITED

Corr, B. E., K. L. Grueber and H. F. Wilkins 1985. Production of 'Sans Souci'. **Minnesota State Florist Bull.** 34(6):8-10.

Dicks, J. W. and A. R. Rees 1973. Effects of growth-regulating chemicals on two cultivars of mid-century hybrid lily. **Scientia Horticulturae** 1:133-142.

Holcomb, E. J. and J. W. White 1970. A technique for soiled application of a growth retardant. **HortScience** 5(1):16:17.

Lewis, A. J. and J. W. White 1981. Improving ancymidol efficiency for height control of Easter lily. **HortScience** 16(1):89-90.

Lewis, A. J. and D. A. Gilbertz 1987. Hybrid lily response to various methods of ancymidol application. **Acta Horticulturae** 205:237-240.

Simmonds, J. A. and B. G. Cumming 1977. Bulb-dip application of growth-regulating chemicals for inhibiting stem elongation of 'Enchantment' and 'Harmony' lilies. **Scientia Horticulturae** 6:71-81.

White, J. W. 1976. *Lilium* sp. mid-century hybrids adapted to pot use with ancymidol. **J. Amer. Soc. Hort. Sci.** 101(2):126-129.

Wilfret, G. J. 1987. Height retardation of Easter lilies grown in containers. **Proc. Fla. State Hort. Soc.**

THE USE OF TISSUE CULTURE IN PLANT IMPROVEMENT

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TISSUE culture techniques can be used to facilitate classical breeding. The first attempt at plant tissue culture began in 1902, when Haberlandt placed the epidermal, pith parenchyma, and palisade cells of monocotyledons in culture. The culture medium contained various sugars, inorganic salts, and amino acids. None of the cells, however, divided. The first successful attempt at tissue culture was made in 1904, when Hannig, using similar media, was able to grow whole plants from embryos (Griesbach 1987).

Many wide crosses fail to produce viable progeny. In some instances, the embryo does not develop. In most cases, however, the embryo develops normally. Viable seed is not obtained because the endosperm fails to develop properly. The endosperm supplies the embryo with nutrients needed for germination and elongation; one can rescue embryos from seeds which lack functional endosperm, by placing the embryo on a nutrient, tissue culture medium. Embryo rescue is an older technique which is still quite useful for plant improvement. Embryo rescue was first described in the early 1900's. Embryo rescue techniques were required for interspecific *Impatiens* hybridization. Essentially, all orchid seedlings are now being raised through aseptic embryo culture. The techniques are so successful that many amateur orchid breeders actually "sow" their own seed at home under innovative aseptic conditions. There are many other examples of embryo rescue being used to produce wide hybrids (Griesbach 1986).

In vitro embryo culture can also be used to rescue embryos from dormancy and long term seed maturation. Most immature embryos are not dormant and will readily germinate in vitro. This fact has been used to breed temperate wildflowers. The requirements to break the dormancy of mature *Cypripedium* seed are unknown and seed rarely germinates. Embryos cultured immediately after seed coat maturation, however, germinate quite readily. There are many other examples such as *Anigozanthos*.

In many woody plants, there is a long time lag between pollination and the appearance of growing seedlings. It has been estimated that the use of embryo rescue and greenhouse culture of seedlings could cut the generation time for commercial rose breeders by at least one half. Orchids are another example where embryo rescue is being used to reduce generation time.

Wide hybridization is usually not the final step in a planned breeding program. Wide hybrids are usually very difficult to use directly in a breeding program to improve flower varieties. The parents' dissimilarities may cause problems with the offspring, such as deformities, reduced vigor, developmental abnormalities and sterility (Griesbach 1984, Griesbach *et al.* 1981).

Another problem associated with successful wide hybridization is that the whole genome (a unit which contains all of a plant's genes) instead of individual desirable genes are transferred. The hybrids are usually intermediate between the two parents. This means that several subsequent generations devoted to backcrossing and selection are required before the undesirable genes are eliminated from the new hybrid.

The reason that most wide hybrids are sterile is because of the lack of chromosome pairing during meiosis. In wide hybrids the parental chromosomes are usually too dissimilar to pair. The reduced pairing leads to non-viable pollen and egg cells which either lack or have extra chromosomes. If the chromosome number of the hybrid is doubled to produce an allopolyploid, then a pair of homologous chromosomes is created and fertility is restored.

There are two ways to produce polyploid hybrids. One method is not very reliable and depends upon rare unreduced gametes. This is probably the mode of origin of most naturally occurring polyploids. In every seed capsule, there might be a few polyploid seeds which result from the chance functioning of unreduced gametes. Triploidy would be the commonest occurrence (one diploid gamete plus one haploid gamete). Two unreduced gametes uniting to give a tetraploid would be a very rare event, indeed. It is very difficult to select these uncommon seeds. The most reliable method for producing polyploid is through chemical treatment with 0.05% colchicine for 1-2 cell generations. Not all allopolyploids, however, are fertile. A classic example is *Lilium*×'Black Beauty' (*L. speciosum*×*L. henryi*).

One potential solution to the sterility associated with wide hybridization would be to artificially induce somatic recombination and chromosome elimination in the hybrid cells or plants. Through the use of tissue culture and several drugs which are known to induce either chromosomal recombination or reduction, it may be possible to induce a meiotic-like process in somatic cells or tissues. In this way, the breeder could achieve introgession, even though the wide hybrid initially may be sexually sterile (Griesbach 1983).

Several drugs are capable of inducing somatic recombination but not chromosome reduction. Caffeine and actinomycin are known to increase the frequency of somatic crossing-over; however, a few chemicals cause chromosome elimination but not somatic recombination. In some instances, colchicine and p-fluorophenylalanine and grieseofulvin can reduce the chromosome number of somatic cells (Griesbach *et al.* 1983).

In summary, there are many less sophisticated tissue culture techniques which can easily be used to facilitate a classical plant breeding program. In most instances, sophisticated gene transfer technology can not be broadly and easily applied to most crops.

LITERATURE CITED

Griesbach, R. J. 1983. Somatic meiosis. **Proc. Inter. Plant Prop. Soc.** 33: 398-402.

———— 1984. An introduction to somatic cell genetics. **HortScience** 19: 367-371.

———— 1985. Polyploidy in *Phalaenopsis* improvement. **Jour. Heredity** 76: 74-75.

———— 1986. Orchid tissue culture. In: **Tissue Culture as a Plant Production System for Horticultural Corps.** ed. R. Zimmerman, *et al.* Martinus Nyhoff Publ., Netherlands. pp. 343-349.

———— 1987. Methods in plant tissue culture. In: **Food Biotechnology**, ed. D. Knorr. Marcal Dekker, Inc., New York, pp. 271-286.

Griesbach, R. J., P. J. Koivuniemi and P. S. Carlson 1981. Extending the range of plant genetic manipulation. **BioScience** 31: 754-756.

Griesbach, R. J., L. Schnabelrauch and K. C. Sink 1983. Griseofulvin-induced chromosome instability and reduction in a *Petunia* somatic hybrid. **J. Amer. Soc. Hort. Sci.** 108: 716-720.

BIOTECHNOLOGICAL BREEDING TECHNIQUES FOR *ALSTROEMERIA*

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THE American Floral Endowment, the NE-169 regional project, and the universities associated with the authors of this paper have supported research with *Alstroemeria*, the Inca Lily, since 1985. This research includes studies with the plant's nutrition, growth regulator applications, soil cooling for extended flowering, and scheduling as a potted crop. Most of the research has centered around the breeding of this beautiful plant for new flower colors and forms, plant heights, fragrance, and longer flowering. Our research with *Alstroemeria* is a coordinated, group effort between 3 universities.

The genus *Alstroemeria* consists of approximately 60 species of rhizomatous herbaceous plants (Bailey and Bailey 1976). Most species are native to Chile and Brazil, but some are found in Argentina, Peru and Bolivia (Wilkins and Heins 1976). *Alstroemeria* was first described by R.P. Louis Feuillet in 1714 after he traveled through South America, but it was eventually named for Don Claudius Alstroemer who sent seeds and descriptions of the plants to his former instructor, Linnaeus (Stinson 1942). Previously, the genus had been classified in the Amaryllidaceae and Liliaceae, but currently they are in their own family, Alstroemeriaceae (Vonk Noordegraaf 1981). Bailey and Bailey's (1976) description of the family follows:

Alstroemeriaceae Dumort. Alstroemeria family

Monocot; 4 genera and over 180 species of rhizomatous herbs with fibrous roots or tubers and erect to climbing leafy stems, native to tropical and subtropical America; leaves alternate, parallel-veined, entire, often resupinate; flowers in a terminal bracted cluster or irregular raceme, bisexual, regular or nearly so perianth segments, separate, in 2 series, stamens 6, anthers erect, ovary inferior, 1-3 celled, ovules many; fruit a capsule. Formerly included in the Amaryllidaceae, but differing in having stems leafy and inflorescences not strictly umbellate. Alstroemeria and Bomarea are cultivated.

The Inca Lily *(Alstroemeria)* produces underground rhizomes which branch sympodially. Root systems are fibrous and produce thickened storage roots with high starch contents; these storage roots are edible. Aerial shoots arise from the rhizome, and lateral rhizomes develop from the second node of the aerial shoot. As a shoot develops, its leaves rotate 180° at their bases so that the adaxial surface faces down. Shoots are vegetative or reproductive. Flowering stems produce a whorl of cymes with each cyme producing one to five flowers. New flowers

* Presentor

arise in the axil of a bract found on the pedicel of the preceding flower (Healy and Wilkins 1985).

The Inca Lily was cultivated only as a garden plant from the time it was discovered until the 1950's , when J.A.M. Goemans began developing hybrids for cut flower production (Goemans 1962). Subsequent breeding via hybridization and X-ray mutation of rhizomes was done by the van Staaveren Company in the Netherlands (Broertjes and Verboom 1974). The origin of many commercial cultivars is uncertain. Most were derived from interspecific hybridization with unreported parentage, and many are sterile triploids from crosses of spontaneous tetraploids with diploids (Heins and Wilkins 1979). The realization by American growers that this plant has tremendous potential to be developed for and grown in the United States, was as is so many other things, late in coming. The Dutch were far ahead of us in this realization and had begun their breeding at least a decade earlier.

The Alstroemeria's increasing popularity with growers as a cut flower can be attributed to its extensive selection of large and colorful flowers, its long post harvest life (approximately 14 days), the absence of major disease or insect pests, and its ability to grow at low greenhouse temperatures. Growers can get a good return on their investment with this plant because the quality of the flowers grown in the U.S. far exceeds that of those which are imported to the U.S. The possibility of growing this plant as potted crop (Bridgen 1986, 1987a, 1987b) or as a garden flower has also stimulated interest and demand for new cultivars in the United States.

Many of the valuable commercial cultivars of *Alstroemeria* are protected from asexual propagation of the rhizomes with patents and from sexual propagation with flower sterility. Initially, we wanted to use individual cells from inflorescences of these plants to develop new flower colors and growth habits. We hoped to develop cultures of callus, which are unorganized, partially differentiated masses of cells. These cells could then be encouraged to mutate by subjecting them to various chemical mutagens such as ethyl methyl sulfonate or colchicine and physical mutagens such as gamma rays and X-rays. However, a major part of this program was to make the callus cells regenerate into plantlets after the chemical treatment, and this could not be accomplished readily.

Then, in 1985, we obtained a dwarf cultivar named 'Rosy Wings'. It is an unprotected cultivar and one that is fertile. Initially, we purchased this plant to evaluate its performance as a 6″ potted crop. In addition to developing the first schedule for growing *Alstroemeria* as a 6″ potted crop that following spring, we repeated all of our laboratory procedures with these plants and found that the ovules were embryogenic. Individual ovules, when placed on a sterile nutrient medium and presented with the optimum environmental situation, will divide and develop into somatic embryos. Somatic embryos are entire plantlets which grow without the union of gametes, as is the situation for zygotic embryos.

We found from these 'Rosy Wings' that fertile plants are more responsive to these procedures than sterile plants. We discontinued using any of the commercial cultivars at that time and concentrated on fertile species. We had been collecting fertile, South American species from collectors and botanical gardens in the U.S., but the selection was limited. We had *A. ligtu* hybrids, *A. psittacina* (*A. pulchella*) *A. violacea*, *A. pelegrina* 'Alba', *A. haemantha*, *A. caryophyllaea*, *A. pygmaea*, and *A. patagonica*.

In 1987, Fred Meyer and I went to Brazil to search for new germplasm. We traveled to Brazilia, Goiana, and San Paulo and collected the fragrant species *A. caryophyllea*, which has a delicate scent similar to that of a carnation. We also collected seeds from an unidentified orange-flowering spp. and an unidentified yellow-flowering spp.

Then in 1988, I traveled to Chile to collect species. In southern Chile, near Orsono, I collected the orange-flowering *A. aurea*. Farther north in Los Logos, the yellow-flowering variation of *A. aurea* was collected. Near Chillan, I found the pale pink-flowering species *A. presliana* var. *presliana*. In the mountains around Santiago, I found a very beautiful species called *A. revoluta*. It has a very long inflorescence with many pale purple flowers on each inflorescence. Several unidentified species were also collected. I never considered myself a taxonomist, but these collections have started a new hobby for me!

The addition of fertile species to our collection allowed us to incorporate traditional breeding procedures into our program. The flowers of *Alstroemeria* are easy to pollinate. They are protandrous: the pollen dehisces before the style is receptive. When the tripartite stigma reflexes it is ready to be pollinated.

We found species of Brazil and Chile to be very recalcitrant, as far as seed set is concerned. Florescence microscopy demonstrated that pollination and fertilization does occur with the different species, however, seeds set is rare. Therefore, we resorted to ovule rescue procedures. The initial procedures for ovule rescue and somatic embryogenesis are essentially the same. Therefore, the information for both are presented together.

The procedure for somatic embryogenesis and ovule rescue begin by removing the ovary 3 to 7 days after pollination. The ovary is surface sterilized in 5.25% sodium hypochlorite for 10 to 15 minutes. It is then rinsed twice in sterile distilled water. The ovary is aseptically opened and individual ovules are removed. For somatic embryogenesis (Winski and Bridgen, 1988) the ovules should be placed on a medium with Murashige and Skoog salts and vitamins plus 1-3% sucrose. They should be placed in the dark for 4 weeks followed by light until somatic embryos form in the next two weeks. For ovule rescue (Winski and Bridgen, 1988), the same procedures should be used, but embryo germination will begin in 3 weeks. Plantlets can be placed in the light after germination begins. Success percentages for both procedures are 10-15% and 5-10%, respectively.

Micropropagation is the rapid, asexual propagation of plants on a nutrient medium *in vitro*. This is one part of biotechnology which has been very helpful for our program. Traditional propagation of *Alstroemeria* by rhizome division is very labor intensive and slow. One rhizome division will take about 8 weeks to produce 3 to 6 new plants. By micropropagating *Alstroemeria*, 4 to 8 divisions can be produced every 4 to 6 weeks continuously during the entire year. The optimum medium for micropropagation of the Inca Lily is full strength Murashige and Skoog salts and vitamins, 3% sucrose, 0.01 mg 1-naphthaleneacetic acid (NAA)/liter, 10 mg N-(phenylmethyl)-IH-purin-6-amine (BAP)/L, 100 mg caesin hydrolysate/L, and 1.2 g gelrite/L; the pH of the medium should be adjusted to 5.7-5.8 before autoclaving (Bridgen and Winski 1989).

Now, we are using all of these biotechnological procedures to develop new *Alstroemeria* cultivars. Ovule rescue is being used successfully to obtain fertile inter-and intraspecific hybrids. Somatic embryos are mutated with physical and chemical mutagens to evaluate the degree of somaclonal variation, and micropropagation is used to rapidly propagate new cultivars. Our next step is to develop Inca Lily plants which are free of all pathogens, including viruses.

This work would not have been possible without the assistance of Fred Meyer, Paul Winski, Joe King, Ramona Reiser, and Phil Ormsby.

LITERATURE CITED

Bailey, L.H. and E.Z. Bailey 1976. Hortus Third: A concise dictionary of plant cultivars in the United States and Canada. Macmillan Publishing Co., New York.

Bridgen, M.P. 1986. *Alstroemeria* has pot crop potential. **Greenhouse Grower.** November, p.22.

Bridgen, M.P. 1987a An update on potted *Alstroemeria* production. **CT Greenhouse Newsletter.** 141:1.

Bridgen, M.P. 1987b. Scheduling *Alstroemeria* as a 6-inch pot crop. **CT Greenhouse Newsletter.** 137:8-10.

Bridgen, MP. and P.J. Winski 1989. Influence of environmental factors on stage II proliferation of *Alstroemeria*. **HortScience** 24(3):139.

Broertjes, C. and H. Verboom 1974. Mutation breeding of Alstroemeria. **Euphytica.** 23:39-44.

Goemans, J.A.M. 1962. Breeding of *Alstroemeria*. **Journ. Royal T Hort. Soc.** 87:282-284.

Healy, W. and H.F. Wilkins 1985. *Alstroemeria* culture. **Minnesota Florists' Bulletin.** 33(3):3-8.

Heins, R.D. and H.F. Wilkins 1979. Effect of soil temperature and photoperiod on vegetative and reproductive growth of *Alstroemeria* 'Regina'. **Jour. Amer. Hort. Soc.** 104(3):359-365.

Murashige, T. and F. Skoog 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. **Physiol. Plant.** 15:473-497.

Stinson, H. 1942. Alstroemerids cultivated in the United States. **Herbertia.** 9:41-52.

Vonk Noordegraff, C. 1981. Bloemprodukti bu *Alstroemeria* 'Walter Fleming'. p. 145. Ph.D. Thesis, Agriculture University, Wageningen, The Netherlands.

Wilkins, H.F. and R.D. Heins 1976. *Alstroemeria* general culture. **Florist Review.** 159(4121):30-31.

Winski, P.J. and M.P. Bridgen 1988. Embryo rescue of *Alstroemeria* **HortScience** 23(3):758.

RESEARCH ON MITOTIC AND MEIOTIC POLYPLOIDIZATION IN LILY BREEDING

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THIS short report on our polyploid breeding programme does not pretend to be a review publication on polyploidy, but a brief survey of our work at the Institute for Horticultural Plant Breeding. The direction of our research on polyploid lilies and the results will be given. For a better understanding this article is divided into two subjects: **mitotic polyploidization**, comprising all activities in which artificial chromosome number doubling was accomplished by treating bulb material with colchicine, and **meiotic polyploidization**, a more natural method through which polyploids were obtained by the occurrence of $2n$ or so-called unreduced gametes. The research presented in this paper is part of a larger programme on lily breeding.

MITOTIC POLYPLOIDIZATION

Our first work on polyploidy with lilies dates from 1978. At that time breeding with polyploid lilies was not very popular. We obtained some tetraploid forms of 'Tabasco' and 'Enchantment' of Peter Schenk from the Dutch firm of Bischoff-Tulleken. Under the (Dutch) climate conditions no seed could be obtained from crosses between tetraploids which were obtained after colchicine treatment. In 1979 we made (in fact as sideline of our research) crosses under high temperature conditions (23 °C and 26 °C in the phytotron). And with success! The tetraploid seedlings flowered in 1981 and were surprisingly early-flowering, healthy and strong, in contrast to the diseased, weak parental clones. We made another cross between the tetraploid 'Tabasco' and the triploid 'Fire King'. With use of embryo culture several strong triploid clones were obtained of which 'Vada' was the most striking one (Figure 1). We released 'Vada' together with 32 tetraploid clones to the Dutch private lily breeding companies in 1983.

After this unexpected success our interest in breeding polyploids was growing stronger. The fertility of the tetraploid F_1 seedlings was tested by crossing them back with their parents and with each other. Pollen of some other tetraploids was exchanged with Peter Schenk after which tetraploid 'Connecticut Yankee' could be brought in.

To broaden the genetic basis of our tetraploid breeding programme a number of cultivars (*L. longiflorum*), low light tolerant hybrids and interspecific hybrids (e.g., 'Loblanca' a cross between *L. longiflorum* and the Asiatic hybrid 'Mont Blanc', and hybrids between *L. longiflorum* × *L. candidum*) were treated with colchicine.

Meanwhile, in the breeding programme for low light tolerance (Van Tuyl *et al.* 1985) diploid clones can be selected which can be forced under lower light conditions without bud abortion. However, under those low light conditions the strength of the stem is insufficient. When these selections were tetraploid a combination of the strong stem of tetraploids and low light tolerance could be expected. Selections out of this low light programme which were already released in 1985 to the Dutch breeding companies together with tetraploid F_2 selections. These low light tolerant selections named as 'Orlito', 'Rolito', 'Whilito', 'Yellito' ('lito' means light

Figure 1. 'Vada' ($2n=36$), a triploid hybrid from the cross 'Tabasco tetraploid×'Fire King'.

Figure 2. 'Connecticut King', the original diploid cultivar (left, 2n=24) and the colchicine-induced tetraploid version (right, 2*n*=48).

Figure 3. 'Loblanca', a interspecific hybrid between *L. longiflorum* and the Asiatic hybrid 'Mont Blanc'

tolerant, and the preposition indicates the colour of the selection) were therefore treated with colchicine. It took us three years to investigate and select the tetraploid forms. From these results some general conclusions could be drawn:

* Difference between genotypes in sensitivity for colchicine treatment can be very large.
* *L. longiflorum* is least sensitive, the Oriental hybrids are most sensitive to colchicine.
* The percentage of tetraploids found after investigation varied between genotypes from 0–50%!
* In the most suitable treatment the colchicine treatment varied between 0.05–0.1 % for 2–8 hours.
* A large variability can be found between selected tetraploid forms of one genotype.

The last conclusion can be explained in terms of difference in fertility and growth vigour. For this reason test crosses were made on a large scale, e.g., between the 18 different tetraploid 'Orlito' and other good fertile tetraploid clones to find the best tetraploid originated from one genotype. These investigations resulted in the release of tetraploid versions of 'Juliana', 'Connecticut King' (Figure 2), 'Mont Blanc', 'Golden Melody', 'Orlito', L. longiflorum 'White American' and *L. longiflorum* "Gelria' and 'Loblanca' (with restored fertility, Figure 3) in 1985 and 1987 (Van Tuyl *et al*. 1987).

Recently we have developed a much faster method of selection of tetraploids. Within three months after colchicine treatment tetraploids can be selected with more accuracy than in the past after two years. This method is based on more advanced instruments like the flow cytometer. A small piece of leaf, root or bulb scale is sufficient to detect the level of ploidy. The procedure is as follows. After colchicine treatment of the bulb scales, the scales are placed in a tray filled with soil or sand with the scales half above the soil. After 2-3 months at 17-20°C in the greenhouse leaves develop, which can be tested first visually. Afterwards the tetraploids can be detected by using the flow cytometer. Applying this method it appeared that in an early stage always many chimeras are found. From the existence of these chimeras it can be concluded that the origin of adventive bulblets from lily scales is in most cases not a one-cell-occurrence. This is contrary to the general opinion up until now. Further we discovered that some of those which were thought to be non-chimeric tetraploids in fact were stable chimeras. Chromosome counts of root tips showed us always real tetraploid cells, while watching the leaves with the flow cytometer it demonstrated a chimeric picture. Last year we solved this problem by testing the stripped epidermis of this chimeras. It appeared that the epidermic layer is diploid while the other layers (including the generative organs) are tetraploid.

We are planning to release a number of tetraploid forms of our diploid low tolerant selections and interspecific hybrids with restored fertility (*L. longiflorum*×*L. candidum*, etc.) in 1990. After this release we will finish this research and concentrate more on the other form of polyploidization: the meiotic one.

MEIOTIC POLYPLOIDIZATION

The meiotic or sexual polyploidization, in contrast to the mitotic, produces polyploids through the fusion of two gametes (pollen or egg cells), one or both having a double number of chromosomes. This research was started because of the great potential of meiotic polyploidization, as a natural method without the disadvantages of colchicine treatment as:

* Occurrence of chimeras,
* Decreased growth and fertility because of the toxic effect of colchicine and the
* Inbreeding effect in contrast to meiotic polyploidization where outbreeding takes place.

From the literature (see the list in Van Tuyl and Kwakkenbos 1986) it is known that unreduced or $2n$ gametes may occur in many species. The frequency, however, is mostly extremely low. In order to trace $2n$ gamete producers within Asiatic lilies, we screened diploid parental plants as follows. Twenty diploid clones were crossed with tetraploid parents under normal Dutch greenhouse conditions (17-20 °C). Over 500 of these ($4x \times 2x$) and ($2x \times 4x$) crosses resulted, because of the 'triploid block' (under the Dutch cool climate conditions) in only about 3,000 seeds. Only 130 of these seeds germinated. Most of these appeared to be diploid seedlings, probably originated from a $2x \times 2x$ cross; 39 probably tetraploid seedlings were tested by crossing them with tetraploid parents. In 16 crosses this resulted in a good seed set, indicating their tetraploid character. For most of these seedlings this could be confirmed by chromosome counting or flow cytometry. In one case a triploid plant was detected. It can be concluded that within the asiatic hybrid group production of $2n$ gametes is rare. Only one parent appeared to be responsible for most of the detected tetraploids namely 'Connecticut King' and even for this cultivar the percentage $2n$ gametes must be estimated below 1%. For the other parents used it should be lower than 0.1%. For this reason 'Connecticut King' was also used to study the influence of temperature on $2n$ gametes production. In a temperature range from 14 °C, to 18 °C, and 22 °C to 26 °C and increasing percentage of dyads in the pollen mother cells was found, indicating the formation of $2n$ gametes (Van Tuyl and Stekelenburg 1988).

Different results were obtained when interspecific hybrids were investigated. Wide interspecific lily hybrids are usually completely male and female sterile. In rare cases, however, some fertile pollen can be detected. In a group of more than 50 embryo cultured hybrids of the cross *L. longiflorum*×*L. candidum* only one hybrid showed a pollen fertility of 25%. Meiotic studies revealed general irregularities during meiotic division. All pollen produced in this hybrid contained $2n$ divisions. Comparable results were found in the interspecific hybrids 'Shikayama' (an Oriental hybrid)×*L. henryi* and *L. auratum*×*L. henryi*; used as pollen parents on Oriental hybrids, they produced, using embryo culture, triploid progenies. Backcrossing these triploids with *L. auratum*×*L. henryi* gave a number of aneuploids with a chromosome number between triploid ($3x = 2n = 36$) and tetraploid ($4x = 2n = 48$) (Figures 4a/4b). In contrast to the wide interspecific hybrid, seedlings from the interspecific cross of the Asiatic hybrid 'Enchantment' and the related *L. pumilum*, produced fertile pollen. Meiotic studies of several of these hybrids revealed, that not only haploid pollen was formed buy a relatively high percentage of $2n$ pollen as well. Flow cytometry results demonstrated in some hybrids a percentage $2n$ pollen, up to 34%. Because of the 'triploid block' in lily the 'Enchantment×*L. pumilum* hybrids, used as pollen parent with diploid Asiatic hybrids, produced diploid and as well as tetraploid progeny. Some of these early flowering tetraploid clones from the cross 'Enchantment'×('Enchantment'×*L. pumilum*) with the intense colour of *L. pumilum* were released in 1985 and named as 'Pumenta', 'Puchanta' (Figure 6) and 'Pumivetta' (Van Tuyl and Kwakkenbos 1986).

In the near future our research will be focused especially on the meiotic form of polyploidization. The important directions in which our research will be tracing more sources of unreduced gametes and studying the mechanism of $2n$ gamete formation.

Figure 4. Polyploid interspecific hybrid derived from *L. auratum*×*L. henryi*: 'Journey's End'×*L. auratum*×*L. henryi* (4A, $2n=36$) and 'Journey's End'×('Shikayama'×*L. henryi*)×*L. auratum*×*L. henryi*) (4B, $2n=40$).

Figure 5. 'Puchanta' ($2n=48$), a tetraploid hybrid derived from the cross 'Enchantment'×('Enchantment'×*L. pumilum*) due to $2n$ gamete formation

LITERATURE CITED

Kwakkenbos, A.A.M. and J.M. van Tuyl 1986. Tetraploide lelies bieden veel voordelen. **Vakbl. Bloem**. 15: 32-33 and **Bloembollencultuur** 97(16): 16-17.

Van Tuyl, J.M., J.E. van Groenestijn and S.J. Toxopeus 1985. Low light intensity and flower bud abortion in Asiatic hybrid lilies. I. Genetic variation among cultivars and progenies of a diallel cross. **Euphytica** 34:83-92.

Van Tuyl, J.M., A.A.M. Kwakkenbos and M.P. van Dien 1987. IVT Stelt Nieuwe Lelieveredlingsproducten ter Beschikking.

CNB-INFO 321:40, **HOBAHO** 61(1):25, **Bloembollencultuur** 98(15):8, **Vakbl. Bloem**.16:36-37.

Van Tuyl, J.M. and P.M. Stekelenburg 1988. Genotypic and environmental variation in production of 2*n* gametes in *Lilium*. *In*: Sexual reproduction in higher plants (Editors M. Cresti, P. Gori and E. Pacini) Springer Verlag, p. 286.

EVOLUTION OF THE GEOPHYTIC HABIT AND ITS PHYSIOLOGICAL ADVANTAGES

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INEVITABLY, a paper with this title is to a degree speculative, although it is based on such factual information as is available, together with current ideas bearing on the subject. Much of the hypothesis is not testable, although it has some value as a framework, parts of which can be strengthened, modified or replaced as more information becomes available.

The term "geophyte" is a convenient generic word for plants with bulbs, corms, pachymorph rhizomes and tubers, following the classic work of Raunkiaer (1934) who divided plants into morphological types on the basis of their methods of surviving the unfavourable season (perennation). One of his groups was called Cryptophytes, where "The surviving buds or shoot-apices are buried in the ground at a distance from the surface that varies in the different species". They were subdivided into Helophytes (marsh plants), Hydrophytes (water plants) and the Geophytes, which he recognised to be found predominantly in such places as dry steppes, where they form a large component of the flora, and also in places with a long growing season and where the unfavourable period is not a hot dry season but a severe winter. Herbaceous monocotyledons are predominantly geophytes.

THE MONOCOTYLEDONOUS ANCESTOR

There is no unanimity about the ancestors of the monocotyledons. Dahlgren and Clifford (1982) favour a shrublet or subshrub ancestor which in response to a pronounced alternation between wet and dry periods evolved compact underground stems, mainly short or long rhizomes from which herbaceous aerial stems were developed. This was accompanied by a loss of cambial activity, which led to the replacement of a necessarily ephemeral radicle by a rich development of adventitious roots. This view is similar to that of Sargant (1903), that an ancestral form lost its cambium because the production of underground perennating organs was facilitated by cambium-less growth. Holttum (1955) presented a view diametrically opposed to these—the ancestral form had no cambium, which led directly to the development of a continuous sympodial evergreen growth habit in the moist tropics where these plants evolved, a habit ideally suited for the development of resting organs and allowing plants to cope with unfavourable periods when they spread to seasonal climates.

While it cannot be proven that the monocotyledons first flourished in the moist tropics, they are species-abundant in such tropical rainforest understory floras as have been extensively studies (e.g. French Guiana, de Granville 1978) and their predilection for wet sites, such as marshes, swamps and wet savannas, is the basis for suggesting a collective aquatic ancestry, a dogma which would be hard to substantiate (Tomlinson 1980) and equally hard to refute. Good (1966) felt that the tropics were the original home of the monocotyledons because only there can their full morphological range be seen; outside the tropics they are

generally small plants which die down in winter, because their watery tissues are unable to withstand hard frost, limiting their maximum development within latitudes 45°N and S.

In the wet tropics, the majority of monocotyledonous plants exhibit a remarkably uniform growth pattern, based on the almost universal sympodial habit of branching, which, paradoxically, allows the expression of a variety of growth forms, such as bamboos, bananas and pandans, single-stemmed, scandent and tufted palms, orchids, aroids and corm and bulb-forming geophytes. In this situation, the lack of a cambium both limits growth and modifies its extent. There is no zone of cells which allows extension growth to continue indefinitely, or allows any increase in either vascular or mechanical tissue once the radial growth of the stem is complete. The build-up of stem diameter, even to a sizeable trunk, is achieved by the gradual development of primary thickening from a narrow embryonic axis, a process called "establishment growth" by Tomlinson (1980). Involved is the activity of a primary thickening (or flank) meristem, a predominance of radial over longitudinal growth in the apex, resulting in the apical meristem proper being located, often deeply, in the middle of a bowl of tissue. The stem base is shaped like a short inverted cone, with closely spaced nodes. The slowness of this establishment growth, which needs to be completed before flowering, is probably why annual monocotyledons are rare and biennials unknown.

Adventitious buds are limited to nodes, usually one per node, and adventitious roots are restricted to the basal stem nodes. Because of the radicle's initial small size and its inability to grow radially, the plant has to depend on adventitious roots from the lower nodes, and the short internodes allow a large number of roots. In some plants, such roots are supplemented by other modifications (presumably later, evolutionary), such as prop roots, which have a mechanical function in upright plants, especially those with longer basal internodes. Contractile roots and specialized organs, such as the "droppers" of tulips, draw or insert the base of the plant into the soil so that there are more nodes close to or below ground, and increase the possibilities for growing even more adventitious roots.

Once established in this form, growth of the plant is constrained by the strength of the base of the stem and the amount of vascular tissues within it. Branching is severely limited because of the increased demands that would make on the ability of the vascular supply to provide water and nutrients, and eventually on mechanical stability. Shoots therefore have a limited life. This is taken care of in plants of a recumbent habit by rooting at other nodes in contact with the soil, or, more commonly, because most plants grow erect, by replacement branches growing from adventitious buds at the base of the plant, producing such familiar growth forms as tillering in grasses, and the familiar and common clumped or tufted growth, typical of monocotyledonous plants. The adventitious buds, during their growth into replacement shoots, would be forced initially to grow horizontally, but would thereafter pass through the same process as the embryo axis and end up with the same form, with their own adventitious roots and adventitious buds to repeat the process. This growth pattern, where the limitations of a fixed vascular system are overcome by basal branching, is versatile, and considerably less limiting than even the largest dicotyledons with terminal growth.

CONSEQUENCES OF THE GROWTH HABIT

In such a sympodial system, there are constraints on the growth of adventitious buds imposed by the other parts, i.e., the operation of apical dominance, correlative inhibition or intra-plant competition. Some elements of the sympodium would be inactive (or "dormant"), and these would be at the base of the plant. These inactive apices would normally grow when the dominant shoot flowered, senesced or died naturally (deterministic growth) or was grazed, attacked by insects or fell to some other predation (opportunistic growth).

Such a system is ideal to allow migration from the moist uniform tropical climate to areas with a seasonal climate, or being able to cope with climatic changes in the existing habitat towards some seasonality or periodicity. The required adaptations are that each new lateral growth should arise from an underground bud, should remain as a bud or continue to grow diageotropically (preferably below ground) and should develop storage tissue and reserves adequate to support the plant until the return of favourable conditions. Extreme conditions could then be coped with by the above-ground parts dying down completely, growth being renewed by the underground survival parts. The storage organs also have potential as aids to dispersal, movement being achieved by the plant itself or by man and other animals (see Galil 1961).

REQUIRED PHYSIOLOGICAL SAFEGUARDS

For such a strategy to develop successfully requires a considerable number of physiological and biochemical controls. Little is known about how storage organs evolved, despite their importance as human food. Storage tissues are usually parenchymatous and often associated closely with vascular tissues, e.g. phloem parenchyma, because they need to be easily accessible when the sink is being filled and emptied. Jolivet (1969) emphasizes that two processes are necessary to achieve tuberization, the first is an inhibition of extension growth of the organ concerned, followed by a stimulation of lateral growth. Environmental factors are involved, as climatic signals, especially temperature and day-length, acting via hormonal promoters and inhibitors of extension growth. Growth inhibition, tuberization and entering into dormancy are viewed as successive steps in the same physiological process.

Starch is the most usual food reserve, but glucose, sucrose and highly polymerized glucofructosans, such as inulin, are common. The adoption of a storage-organ strategy requires safeguards to protect and maintain these reserves until required; an outer covering or tunic to restrict water loss, a biochemical means of reducing a high respiration rate, which would otherwise deplete the reserves (especially at high temperatures), a means of protecting the storage organ from frost if this occurs, and some means of deterring other organisms (e.g. insects, fungi) from consuming the reserves, which would be in short supply anyway in the season unfavourable for growth. These requirements have been met in many different ways, as seen by the range of storage organs developed; bulbs, corms, stem and root tubers, rhizomes, with different kinds and numbers of covering structures, the modification of different tissues for storage (leaf bases, scales, stems, hypocotyls and roots) and differences in the longevity of these storage organs. Different groups have evolved various chemicals for repelling or deterring pathogens, such as the familiar "flavours" of onion and garlic, antimitotic agents and oxalic acid in *Narcissus*, poisonous alkaloids in *Crocus* and *Colchicum*, trichosclereids and the tulipalin of *Tulipa*. Respiration rates of storage organs are generally low, and *Tulipa* and *Iris* have low rates at high temperatures (Rees 1972).

A further modification is protection for the emergent shoot at the end of dormancy, usually achieved by its enclosure in scales which emerge with the shoot. In such geophytes as have been examined, there is evidence that conversion of highly polymerized carbohydrates to those of lower molecular mass occurs in response to cold, and has a role in cryoprotection (Hobson and Davies 1977).

A little-studies but important aspect of geophyte growth is the regulation of the sink strengths of the several growth components—shoot, flower, storage organ—which must be balanced, usually by separation of their growth periods, to ensure survival. In *Tulipa*, mother bulb reserves are channelled first to the roots and leaves; the latter after emergence provide a source of carbon for the continued growth of the flower, stem and daughter bulbs until anthesis.

Growth of daughter bulbs and the accumulation of starch during this later period is also supported by the remains of the mother-bulb reserves (Ho and Rees 1976), indicating a dynamic source-sink relationship for carbon transport.

DORMANCY

Removing seasonal and anthropomorphic epithets associated with discussion of dormancy (Lang 1987) is favour of ecodormancy (regulation by environmental factors), paradormancy (regulation by physiological factors outside the affected structure) and endodormancy (regulation by physiological factors inside the affected structure), the axillary buds are paradormant from initiation, but in other cases existing growing organs are transformed for storage. They are released from the dormant state when the inhibition by the actively growing shoot is removed, provided there is no ecodormancy nor endodormancy.

Returning to the hypothetical ancestor moving into an unfavourable period, it is beneficial if the onset dormancy coincides with the start of the unfavourable period, i.e., the plant grows actively until this is prevented by environmental factors, although there are examples where another environmental factor is involved, such as day length in *Allium*. More problematic is the breaking of dormancy. If this were achieved merely by removing the stimulus inducing dormancy (rain following drought, or warm weather replacing cold), then there could be a disastrous result from a short spell of unseasonal weather breaking dormancy prior to a return to adverse conditions. An example of dormancy controlled moisture are the so-called tropical rain flowers *Pancratium* and *Zephyranthes* (Holdsworth 1961). These plants die down at the start of the dry season, but respond to rain by rapid emergence of any flowers which have grown to a critical stage within the bulb. Less developed flowers cannot respond, and are therefore in reserve.

More sophisticated dormancy breaking is common, with regrowth following a stimulus different from that initially causing the dormancy. Many steppe plants endure two consecutive unfavourable seasons, a hot arid summer and a cold winter. A cold requirement of long duration must be satisfied before dormancy is broken, and the fine tuning is provided by ecodormancy imposed by low temperatures in early spring. Field observation is not sufficient to identify causes of dormancy and its breaking because temperature, water-availability and day length do not vary independently, and there are often strong interactions to be unravelled.

ADVANTAGES OF THE GEOPHYTIC HABIT

Dormancy is clearly a method for ensuring survival through an adverse period in the plant's native climate, and as there has been strong selection pressure over long time spans, the plant's "fit" to the environment can be close, while still retaining sufficient variability for the population to have some flexibility.

It is a mistake to consider dormancy as a period where the plant marks time until conditions improve—a form of suspended animation. In many bulbous plants, the apex is active even when the above-ground parts have died, so that although in common parlance the bulb is "dormant", if this state is considered to be a property only of the apex, there is no dormancy. At the expense of food reserves stored during the previous growing season, or even earlier, the apical meristem might be producing scale or leaf primordia or even initiating or completing the development of the flower or inflorescence. By the time regrowth occurs in the spring, in species like *Narcissus* and *Tulipa*, all parts are fully formed, and temperature permitting, the emergence and growth to anthesis is rapid and unchecked. Further, daughter bulbs and other adventitious buds can also be growing during this period, at the expense of previously stored food reserves.

Different strategies have evolved for ensuring survival, consequently, the extent of development occurring within the bulb during the unfavourable period also differs. It has been suggested that the severity and kind of unfavourable period affects the form of the plant response, and in particular the times of flower initiation and anthesis relative to the period of main vegetative growth. Clearly, the possession of considerable food reserves allows flexibility in the timing of flowering, unlike the situation in plants with minimum reserves which are constrained to a period of juvenility to ensure sufficient photosynthetic capacity to support flowering and the subsequent seed development. Aoba (1976) considered that the major climatic types (i.e., Mediterranean, steppe, tropical highland and eastern Asian) imposed different periodicities (growing season) on the life cycles of the native bulbous plants, and also different environmental triggers to induce tuberization and to break dormancy.

Following a different approach, Kamerbeek *et al.* (1970) classified types of dormancy in relation to the tri-phasic development exhibited at the apex of 1) corm or bulb scale initiation, 2) initiation of leaf primordia and stem, and 3) floral initiation. In the first type, where dormancy is most pronounced, and characteristic of *Lilium*, *Allium*, and *Gladiolus*, apical inactivity sets in after the first phase. The dormant period is long and terminated by low temperature, with flower initiation of a fixed but high number of leaves. The second type, exemplified by *Tulipa*, *Narcissus* and *Hyacinthus*, comprises those which show hardly any physiological dormancy, because growth is continuous, provided that temperature allows it, except for stem extension, for which a cold period is essential, after flower initiation, for rapid growth and the realization of full extension potential. The third type exhibits no physiological dormancy, but can be ecodormant, e.g., iris, whose leaves appear before winter sets in. There appears to be no cold requirement for optimum growth, but this is difficult to ascertain because cold is necessary for flower initiation, i.e., true vernalization. Although not specifically stated by Kamerbeek *et al.*, the tropical evergreen bulb plants, such as *Hippeastrum*, must also belong to this type, their "dormancy" in horticulture resulting from imposed constraints of temperature and drought. Such plants often have remarkably regular behavior; in the comparatively constant tropical temperatures, *Pancratium* produces a new leaf each week and seven leaves between inflorescences (Holdsworth 1961).

ACHIEVEMENTS OF THE GEOPHYTIC HABIT

Observations of plants in the wild allows some generalizations. Spring-flowering bulbs are characteristic of areas with wet winters and hot, dry summers; the phenogram of the Mediterranean flora shows a clear peak in spring. The growing season is short and leaves and flowers emerge together. When winters are cold, emergence and flowering are delayed until summer, provided conditions then are not too dry. Autumn-flowering plants occur where mild wet winters are followed by hot and dry summers. Cold winters also seem to favour autumn (fall) flowering, but leaf emergence is delayed until spring. Alternatively, if winters are mild and wet, autumn flowering can soon be followed by leaf emergence. These are broad generalizations; in any habitat it is possible to observe different strategies which also appear to be successful, indicating scope for detailed ecological studies of periodicity, as begun for Israel by Dafni *et al.* (1981a, b).

These authors suggest that hysteranthous behavior (flowering at the end of summer without leaves) has evolved from the basic synanthous (simultaneous appearance of foliage and flowers) in two ways. In one there is delayed flowering (the *Urginea* type, which also includes *Scilla*, *Narcissus* and *Pancratium*) and the other an advance of flowering relative to the leaves, the *Crocus* type (including *Merendera*, *Colchicum* and *Sternbergia*, all of which have subterra-

nean ovaries, an annual storage organ and a small flower stem). The *Urginea* type is seen as an extreme adaptation to a very short and somewhat unpredictable growing season of the Mediterranean region where it borders on more desert conditions. The advantages lie in prompt germination of the non-dormant seed and the early establishment of young plants in the short, wet period and the possibility of better pollination, while larger, and perennial, storage organs improve the chances of survival especially in the more unpredictable climates. The *Urginea* type is apparently common in dry savannas of tropical Africa. The relationship between flowering dates and pollination efficiency is little studied and poorly understood, but in outbreeding, insect-pollinated geophytes it must be important, and flowering time is allowed some versatility by the possession of the geophytic habit.

Associated with the geophytic habit, and the possibilities of a considerable amount of early shoot development during the unfavourable cold period, are large genomes (Grime and Mowforth 1982). This characteristic is found in Mediterranean geophytes and grasses whose growth is confined to the cool conditions of winter and early spring. It is suggested that large genomes have evolved where much of cell division occurs during the warm dry summer, and growth in spring at low temperature is a result of the rapid expansion of these cells. By this temporal separation of cell division and expansion, growth is much less temperature-dependent than if these processes occurred together, and clearly has a strong survival value for plants in a short growing season.

CONCLUSION

From the simple presumed origins of continuous sympodial growth in a uniform climate, and its morphological limitations, have developed the geophytes, a highly complex and successful group of plants, mainly monocotyledonous, which now occur world-wide (except in the Arctic and Antarctic) in a wide range of climates from the uniform moist wet tropics to extremes of high temperature and drought, as well as in temperate areas with some frost. This has been achieved by developing a variety of storage organs, dormancy mechanisms and associated physiology to control the plants' periodicity to match closely the local climatic and edaphic conditions, thereby allowing survival and successful competition with other life forms.

LITERATURE CITED

Aoba, T. 1976. Effects of temperature on the seasonal periodicity of bulb formation in plants. **Environmental Control in Biology**, 14:81-90.

Dafni, A., A. Shmida and M. Avishai 1981a. Leafless autumnal-flowering geophytes in the Mediterranean region—photogeographical, ecological and evolutionary aspects. **Plant Systematics and Evolution** 137:181-93.

Dafni, A., D. Cohen and I. Noy-Meir. 1981b. Life-cycle variation in geophytes. **Annals Mo. Bot. Gard.** 68:652-660.

Dahlgren, R.M.T. and H.T. Clifford 1982. The monocotyledons; A comparative study. Academic Press, London & New York, 378pp.

Galil, J. 1961. Kinetics of Geophytes. Hakibbutz Hameuchad Ltd., Tel-Aviv, 232pp.

Good, R. 1966. The botanical aspects of continental drift. **Science Progress (Oxford)** 54:315-24.

Granville, J.-J. de, 1978. Recherches sur la flore et la vegetation guyanaise. Thesis, Universite des Sciences at Techniques du Languedoc, Montpellier.

Grime, J.P. and M.A. Mowforth 1982. Variation in genome size—an ecological interpretation. **Nature UK** 299:151-3.

Ho, L.C. and A. R.Rees 1976. Re-mobilization and redistribution of reserves in the tulip bulb in relation to new growth until anthesis. **New Phytologist** 76:59-68.

Hobson, G.E. and J. N. Davies 1977. Mitochondrial activity and carbohydrate levels in tulip bulbs in relation to cold treatment. **Journal of Experimental Botany** 28: 559-68.

Holdsworth, M. 1961. The flowering of rain flowers. **Jour. West Afr. Sci. Assn.** 7:28-36.

Holttum, R.E. 1955. Growth habits of monocotyledons, variations on a theme. **Phytomorphology** 5:399-413.

Jolivet, E. 1969. Physiologie de la tuberisation. **Annales de Physiologie vegetale** 11:265-301.

Lang, G.A. 1987. Dormancy; a new universal terminology. **HortScience** 22:817-820.

Kamerbeek, G.A., J.C.M. Beijérsbergen and P.K. Schenk 1970. Dormancy in bulbs and corms. Proceedings of the 18th International Horticultural Congress, Tel-Aviv, 5:233-9.

Raunkier, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford, 632pp.

Rees, A.R. 1972. The growth of bulbs. Academic Press, London & New York, 311pp.

Sargant, E. 1903. A theory of the origin of Monocotyledons, founded on the structure of their seedlings. **Annals of Botany** 17:1-92.

Tomlinson, P.B. 1980. Monocotyledonous habit in relation to morphology and anatomy. In: **Petaloid Monocotyldeons**, Linnean Society Symposium Series 8. Academic Press, London, pp.7-20.

BLOOMING STRATEGIES, FLOWER SIZE AND ADVERTISING IN THE "LILY-GROUP" GEOPHYTES IN ISRAEL

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THE present work studies the relationships between flower size, plant height and the flowering seasonal rhythms of the "Lily group" geophytes in comparison to the whole flora of Israel. The geophytes' flowering peak is earlier (March) than the whole flora (April). They also have a secondary peak in the autumn (October-November) in which they comprise up to 80% of all flowering species in this season. The dominance of blooming geophytes in the autumn under Mediterranean conditions corresponds to the ability of these plants to use their storage reserve to flower in a long dry season. The geophytes have the largest flowers in the flora of Israel.

A significant negative correlation was found between flower size and plant height throughout the year when the autumn flowering geophytes were found to have larger flowers than those of any other season or life-form. The findings are explained in terms of "competitive advertisement" versus "discovery advertisement" which molds the flower size in relation to the dominating factors which are involved in the "pollination market".

Geophytes with white flowers are prominent in the winter; pink, purple and blue are the most common colors throughout the year. Yellow flowers, however, are relatively rare as compared to their share in the whole flora. Although the "Lily group" geophytes are very diverse, some stylized patterns in the flower morphology as well as in morphology, are recognized in connection to the flowering season.

INTRODUCTION

The geophytes comprise 10.1% of the flora of Israel. They appear mainly in the Mediterranean territory and in semi-desert areas (Shmida 1981; Shmida and Burgess 1988; Dafni 1989). The present study deals with the geophytes belonging to the super-order Liliflorae (Dahlgren *et al*. 1985) which includes 138 species of the local flora. The lily group as used in this paper includes the petaloid bulbous monocots, especially Liliaceae, Amaryllidaceae and Iridaceae. Many of these species have showy and attractive flowers and are very prominent in the local flora. The blooming spectrum in the Mediterranean climate shows a peak in spring (Zohary 1962; Auerbach and Shmida 1987), a rhythm which is considered to be adapted to the local seasonal climate (Dafni and Shmida 1989). In the time period between the end of the summer and the end of winter (August-January) there are relatively few blooming species, the majority of which belong to the "lily-group" geophytes (Burtt 1970; Dafni *et al*.

1981b; Strid 1987). Several researchers explain the ability of geophytes to flower outside of the main season in terms of food storage. This reserve enables the plant to separate out the reproductive from the vegetative phase and then to flower in the autumn (Burtt 1970; Pate and Dixon 1982; Dafni *et al.* 1981a; Holdsworth 1961; Rees 1972; Mooney and Billings 1960, 1961). No statistical data on phenology have been issued so far. However, flowering in autumn—a season of harsh pollination environment (Dafni and Werker 1982) is understood as resulting from low competition for pollinators due to scarcity of pollinators (Dafni and Dukas 1986; Dafni *et al.* 1981a, Strid 1987).

MATERIALS AND METHODS

The geophytic flora of Israel includes 165 species. For the present analysis, rare or dubious species were excluded. The final list consists of 138 species. The subalpine species of Mount Hermon (20 species) were also excluded.

The data for the analysis (flower size, plant height, and flowering season) were taken from Zohary and Feinbrun-Dothan (1966-1986), ROTEM Data Base (Shmida and Ritman 1985), and mainly from field samplings carried out by the authors during the last decade. Flower colors were classified according to Dafni and Shmida (1989).

The number of blooming species in each month was scored by the accumulative data of all the flowering species in the same month. Species in which the flowering duration is longer than one month were scored for each month separately. Flower size is expressed by the longest axis regardless of the shape. At least ten flowers from three plants were measured.

Table 1. Systematical aspects of the Israeli geophytes and the taxonomical treatment of the "lily-group" species.

The Family	No. of Species in Israel	Percentage of the Geophyte	The Storage Organ
The "lily-group"			
Asparagaceae	4		Tuber
Ruscaceae	1		—
Ixioliriaceae	1	52.2	Bulb
Asphodelaceae	7		Fleshy roots
Hyacinthaceae	36		Bulb
Alliaceae	38		Bulb
Amaryllidaceae	7	4.2	Bulb
Colchicaceae	10		Corm
Liliaceae	19		Corm, Bulb
Iridaceae	30	15.7	Tuber, Bulb, Rhizome, Corm
Others			
Orchidaceae	29	14.2	Root-tuber, rhizome
Geraniaceae	3	1.4	Corm
Umbelliferae	1	0.5	Corm
Primulaceae	2	1.0	Corm
Compositae	3	1.5	Corm, Tuber
Beberidaceae	2	1.0	Corm
Araceae	9	4.4	Corm, Rhizome
Fumariaceae	1	0.5	Corm
Ranunculaceae	1	0.5	Fleshy roots

Following Dahlgren *et al.* 1985, all of which are included in Liliaceae by Feinbrun-Dothan 1986.

RESULTS

The systematic aspects of the Israeli geophytes are shown in Table 1. This table shows the frequency of geophytes in the main plant families represented in the flora of Israel, in relation to the storage organ type. The "Lily-group" comprises 73.1% of the geophytes of Israel, and together with the Orchidaceae and Araceae (which have mostly deceptive flowers, and thus were excluded from this study) they make up 95.4% of this life-form list.

The monthly blooming spectra of the "Lily-group" species as compared with the rest of the Israeli flora are presented in Table 2 and in Figures 1 and 2. From these data the following conclusions may be reached:

1. The peak flowering of the "Lily-group" occurs in March (22.6% of the group) while the whole flora peaks in April (36.4%) (Figure 1).
2. The number of flowering "Lily-group" species increases from September to March and then drastically declines, reaching zero flowering in July (Figure 1).
3. Very few species, out of the whole flora, flower during September to January (0.2% to 0.7% of the total flora excluding the "Lily-group"). The relative share of the "Lily-group" flowering species is significantly higher during the period of September (24.3%) to February (22.5%), peaking in November (80% of the whole blooming species of this month). From March to August the relative number of blooming "Lily-group"species is low (4.3% to 7.9%) in comparison to the whole flora (Figure 2).

It can be seen (Table 2) that the monthly rhythm of the "Lily-group" species shows a similar pattern under Mediterranean as well as under desert conditions. The strong deviation in May (14 species in the Mediterranean versus 1 species in the desert) is contributed by *Allium* spp. Anyway, the flowering "Lily-group" geophytes are rare in both regions from June to August.

Color analysis of the "Lily-group" species as well as of the whole flora is represented in Table 3. The main points are:

1. Only three species, peaking in March (*Tulipa* spp.) have red flowers (a phenomenon which is related to beetle pollination (see Dafni *et al.* 1990)). This color is also rare in the whole flora (1.8%).
2. There is a relatively high proportion of blue "Lily-group" flowers (9.2%) as compared to the whole flora (4.7%),. The blue species (*Muscari parviflorum Iris vartani, I. regis-uzziae, I. histrio, Allium hierochunticum* and *Hyacinthus orientalis*) flower in January-February.
3. Pink flowers appear in similar proportions (26%) in the "Lily-group" and in the flora as a whole. The pink species peak during April-May (28.6%—29.2%) (Dafni and Shmida 1989) while the pink "Lily-group" flowers peak primarily in November (50%) and secondarily in April (33% of the group).
4. There are relatively few "Lily-group" species having yellow flowers (9.9%) as compared to yellow ones in the whole flora (25.3%). The yellow flowers are mostly *Gagea* (6 species) which flower mainly in February while the peak of the whole yellow flowers occurs in April (Dafni and Shmida 1989).
5. The main bordeaux "Lily-group" flowers (13% compared to 2.8% in the whole flora) are contributed especially by the "multicolor" species of *Iris* (Section Oncocyclus) which flower from March to April.

6. Most of the white "Lily-group" flowers are big, showy and appear during September (37.1% of the group) (e.g. *Pancratium* spp., *Crocus* spp., and *Ornithogalum* spp.). The peak of the white flowers of the whole flora is in April (Dafni and Shmida 1989).
7. Flesh-colored flowers are mainly inconspicuous ones of *Allium* (8 species), *Scilla* (2 species) and *Urginea undulata*. This color is more common in summer, during May (31.6%) to September (50% of the "Lily-group") and is rare (4.7%) in the flora as a whole.

The analysis of the monthly distribution of the floral size and the plant height, regarding the "Lily-group", is presented in Table 4. From these data one could point out that:

1. On the average the "Lily-group" have larger flowers (26.5±9.5mm) than the average ones in the whole flora (15.7±8.6) (see also Figure 4).
2. The plant height gradually increases from October reaching its peak in June. The range of average plant height of the "Lily-group" species is 6.5cm in October up to 80.0cm in June.
3. A negative correlation is evident ((x = -1.56y + 73.1; r = 0.62; p= 0.05, Figure 3) between the plant height (y) and the flower size (x) in the "Lily-group" species.

Analysis of the flower size in accordance with the life form in the whole flora of Israel is shown in Figure 4. It can be seen that the geophytes have, on the average, the largest flower size in comparison to all other life forms present in the flora of Israel.

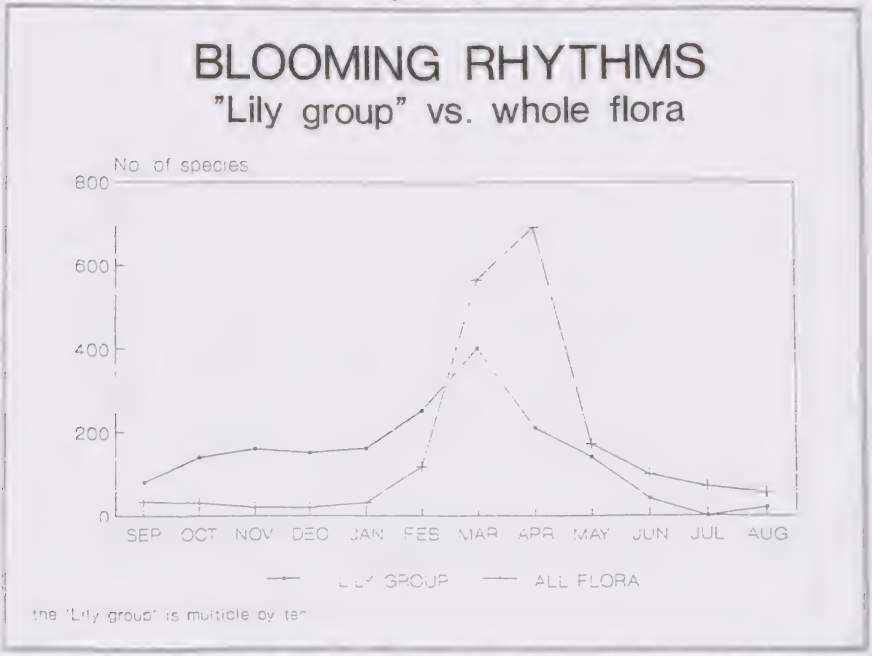

Figure 1. The monthly blooming rhythms of the "Lily group" species as compared to the whole flora of Israel. (Note The "Lily-group" value is a multiple of ten).

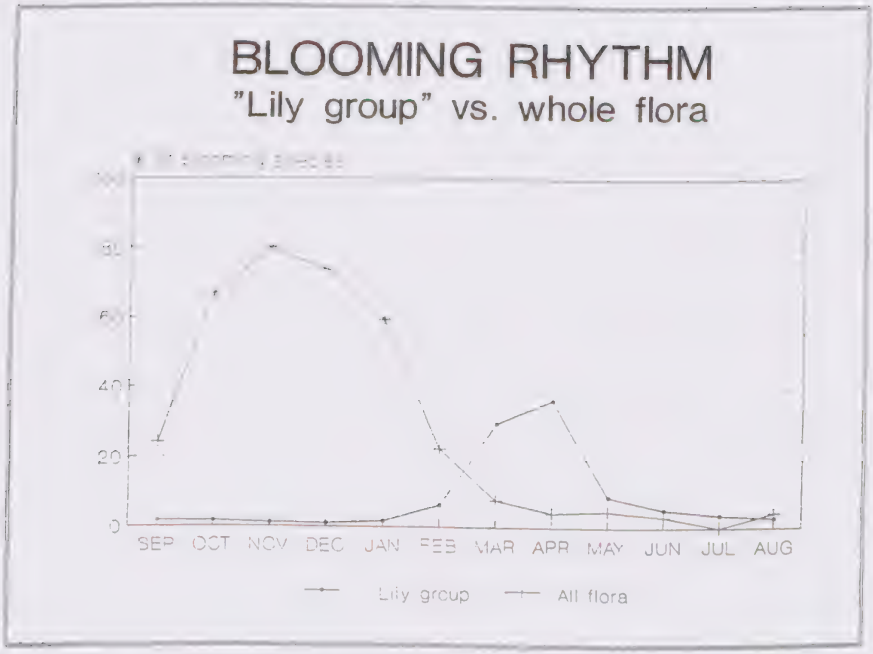

Figure 2. The relative monthly blooming rhythms of the "lily-group" species as compared to the whole flora of Israel.

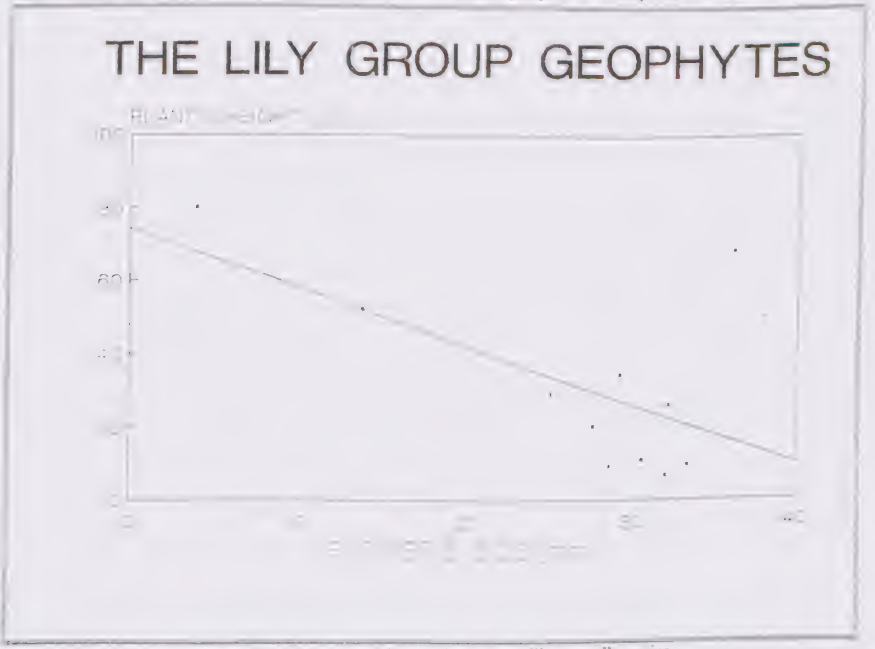

Figure 3. The relation between plant height and flower size in the "lily-group" species.

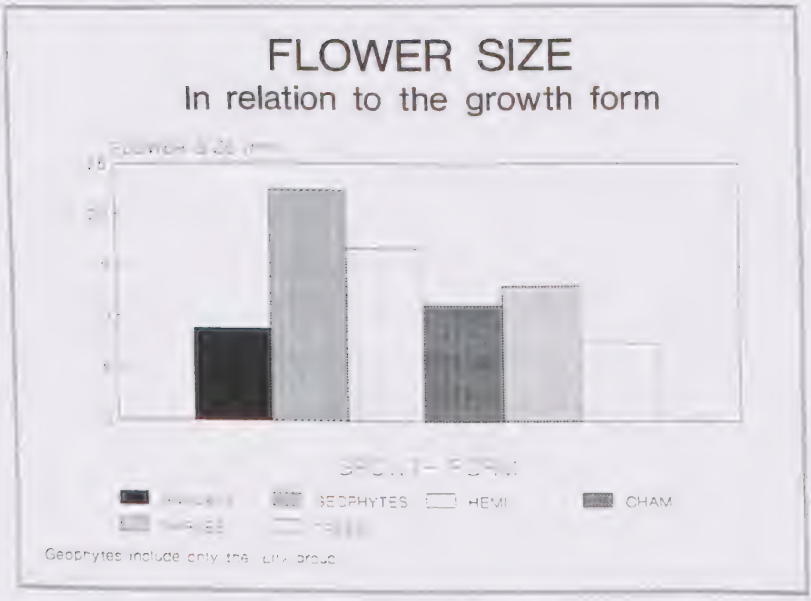

Figure 4. Flower size in relation to growth form in the flora of Israel. (Note: The geophytes include only the "lily-group" species).

Table 2. The monthly blooming rhythm of the flora of Israel and of the "lily-group" geophytes

Month	A	B	C	D	E	F	
						F_1	F_2
Jan.	30	16	1.6	59.3	9.1	11	5
Feb.	117	25	6.2	22.5	14.3	19	9
Mar.	564	40	29.7	7.9	22.6	30	15
Apr.	692	21	36.4	4.1	12.0	16	6
May	171	14	9.0	4.7	8.0	14	1
June	98	4	5.2	3.2	2.3	4	0
July	68	0	3.6	0	0	0	0
Aug.	54	2	2.8	4.3	1.1	2	1
Sep.	33	8	1.7	24.3	4.6	5	4
Oct.	30	14	1.6	66.6	8.0	10	2
Nov.	20	16	1.1	80.0	9.1	14	2
Dec.	19	15	1.0	73.6	8.6	11	4
	1896(1)	175(1)					

A No. of blooming species: all flora.
B No. of blooming "lily-group" species
C % of blooming "lily-group" flora blooming in the month out
D % of the "lily-group" blooming species out of the all flora in the month
E % of the "lily-group" flora blooming in the month out of all the "lily-group" species
F No. of blooming ** "lily-group" species (F1 = Mediterranean; F2 = Desert)
**Some species are present in both regions.

(1) The number represents the sum of scores and is higher than the actual inventory of species since some have peak flowering of more than one month, and hence they were scored accordingly.

Table 3. The monthly distribution of the flower colors of the "Lily-group" species.

		1	2	3	4	5	6	7	8	9	10	11	12	Σn	%	%
Red	No.	0		3										3	2.2	1.8
	%			6.5												
Blue	No.	3	6	2	1						1	1	1	12	9.2	4.7
	%	17.6	21.4	4.3	4.2						7.1	6.3	6.7			
Pink	No.	3	5	11	8	3	1				5	8	6	34	26.0	26.7
	%	17.6	17.6	23.9	33.3	15.8	16.7				35.7	50	40			
Yellow	No.	2	4	3	1	1					1	2	1	13	9.9	25.3
	%	11.8	14.8	6.5	4.2	5.3					7.1	12.5	6.7			
White	No.	8	9	14	6	3	1		1	3	4	4	7	34	26.0	19.8
	%	47.1	32.1	30.4	25.	15.8	16.7		50.	37.5	28.5	25.	46.7			
Cream+Green	No.	1	1	4	1	3				1	1			6	4.6	11.4
	%	5.9	3.5	8.7	4.2	15.8				12.5	7.1					
Bordeaux	No.		2	8	5									17	13.0	2.8
Flesh	No.		1	1	2	6	4		1	4	2	1		12	9.2	4.4
	%		3.5	2.2	8.3	31.6	66.7		50.	50.	14.3	6.3				
Scores		17	28	46	24	19	6	0	2	8	14	16	15	131		
Σn		16	28	46	21	14	4	0	2	8	14	16	14			
#of all ANIPOL blooming species		30	117	569	692	171	98	68	54	33	30	21	19	1537 species 1901 scores		

No = Number of species
% = Percentage out of all the flowering species in the same month
% = ANIIPOL = Animal-Pollinated species.

Table 4. The monthly distribution of flower size and plant height in all the flora of Israel and in the "Lily-group" species.

Month	Average flower size (mm)		Average plant height (cm)	
	All flora	Lily group	Lily group	All Flora[2]
Jan	20.3	28.5	9.1	15.4
Feb.	14.8	27.5	20.3	16.3
Mar.	13.2	24.9	29.2	21.2
Apr.	12.9	29.1	34.3	27.8
May	9.0	13.7	52.1	50.9
June	7.7	3.9	80.1[1]	54.9
July	6.7	—	—	58.5
Aug.	6.4	36	68.0	60.7
Sep.	17.2	32.1	25.8	40.0
Oct.	23.1	33.3	9.4	10.6
Nov.	30.5	32.0	6.5	9.3
Dec.	27.1	30.5	10.9	10.2
$\mu \pm SD$	15.7±8.4	26.5±9.5		

[1]Contributed mainly by *Lilium candidum* which may reach a height of 2m. Without it the average value is 60.1cm.
[2]Only animal pollinated species, wind-pollinated were excluded.

DISCUSSION

The Blooming Rhythm of the "Lily-Group" Geophytes

The existence of a storage organ provides the geophytes with a potential ecological advantage: the ability of separation between the vegetative and the reproductive phases (Dafni *et al.* 1981a,b; Svoskin 1960; Burtt 1970; Evanari and Gutterman 1985), and to flower far beyond the growth season. Geophytes in Israel flower in spring too, but they are relatively prominent mainly between September and February (Dafni 1989 and see Table 1 and Figure 2).

The possible advantages of flowering outside of the main season (spring) are twofold:

1. Previous workers did not specify the quantitative relations between the frequencies of pollinators and flowers which mold the autumnal pollination market. The argument was that a shift of the flowering season from the main season (spring) to the autumn would be advantageous in terms of competition for pollinators (Burtt 1970; Strid 1987; Dafni and Werker 1982; Dafni and Dukas 1986; Shmida and Dukas 1986, 1989). The hidden assumption was that the chances for visitation frequency per flower out of the main flowering season is higher when flowers are scarce due to less competition.
2. The "pollination market" (Selten and Shmida 1989) in autumn is depauperate in flowers as well as in pollinators. Such a market will be termed as a "shrunken market". In every habitat there are generally only one to three co-blooming species which appeal mainly to generalist pollinators such as solitary bees and flies. Such a situation enhances the chances for a "non-mixed visit" in the same foraging bout among different plant species, leading to a high degree of "forced" constancy and, thus, eventually to pollinators' higher constancy (Waser 1986). The result is a very low rate of improper pollen transfer (see Rathcke 1983).

The "Lily-group" autumnal flowering species are pollinated mostly by a few insect species. Such is the case for *Urginea maritima* (Dafni and Dukas 1986), *Sternbergia clusiana* (Dafni, and Werker 1982), *Pancratium parviflorum*, *Scilla autumnalis* (Dafni, unpublished), *Colchicum* spp. and *Crocus* spp. (Shmida and Dafni (in preparation)—all of which are pollinated by generalist solitary bees and syrphids which exploit any available floral resources. Generally there is no specificity between the flower and the pollinator: the nectar as well as the pollen are exposed, and the flower rewards are available to almost every visitor. The common solitary bee genera in this season are *Lassioglossum*, *Ceratina*, *Nomioides* and *Hylaeus*. *Pancratium maritimum* is pollinated by hawkmoths (Eisikowitch 1971) and is limited to a specific habitat (seashores).

We tend to emphasize the second reason as a major factor favoring autumnal flowering, especially under dry Mediterranean conditions. Competition could, however, serve as a complementary driving force leading to a shift in the blooming season.

A similar situation exists in the winter (December-January) in the Mediterranean mountain territory where the prevailing low temperatures delay the blooming of all other life-forms except the geophytes (Figure 1) which can use the already accumulated reserve to flower in this harsh season.

One may ask why so few geophytes flower during May to July (0 to 14 species), a period in which there is a maximum abundance of insects and a relatively low abundance of flowers (Shmida and Cohen 1989). An analysis of the monthly flowering rhythms (Table 2) reveals that there are still 68 to 170 other flowering species which are able to compete with the geo-

phytes. Thus, it seems to be more advantageous for a geophyte to flower in a season in which very few other species are blooming (September-February).

The "Flowering Market", Flower Size and Reward.

The leading factors which mold the "pollination market" (Selten and Shmida 1989) are in a trend of change throughout the year, thus imposing different pressures on the flower size and reward in the various seasons (Shmida and Cohen 1989). During the peak of the flowering season (March-April, see Figure 1), a relative surplus of flowers can be found, as compared to pollinators. This can be analogous to a "competitive market of buyers" (Tirole 1988). This situation creates high competition among the flowers in attracting pollinators. The ultimate result is a large investment in reward (nectar and pollen)as well as in advertisement (e.g., large flowers) (Shmida and Cohen 1989). In general, the spring "competitive market" is determined more by the "buyers", the pollinators which dominate the market. Therefore, it is expected that the plants will invest more (relative to the vegetative structures) in their flowers (advertisement and reward). This may explain why spring flowers are generally larger and more rewarding than flowers in any other season (Shmida and Cohen 1989).

Towards the beginning of the summer (May-June) the situation in the Mediterranean "pollination market" reverses itself sharply. A shift occurs from a market of "buyers" to that of "sellers", namely, a surplus of insects over flowers is evident (Shmida and Dukas 1986). Under these conditions one would expect to find a reduction in the floral investment (reward as well as advertisement). The result is a reduction of the average flower size (Table 4) in the whole flora as well as in the "Lily-group" species.

A totally different situation exists from October to December. Our data clearly indicate (Table 4) that the average flower size of the "Lily-group" species is larger than any other season. *Crocus nyemalis*, *Crocus olbanus*, *Colchicum decaisnei*, *Colchicum hierosolomitanum* and *Sternbergia clusiana* will be noted as having large showy flowers (see also Mathew 1987; Mathew and Baytop 1989). The mean expected distance between each flower pair in the field is large, due to their low abundance, which renders the situation from a "competitive advertisement" to a "discovery advertisement". Under these circumstances the large geophyte flowers found (Table 4) are a result of a "discovery advertisement" and not of a "competitive advertisement". Large flowers are thus expected to have small reward, while the flower's size attracts the visitors from a distance. Since transportation cost is high anyway, the pollinator will ignore the low rewarding flowers due to the relative scarcity of flowers at all. " Competitive advertisement" is a situation which happens in spring where a market of many flowers compete for a limited number of pollinators. The flower color and size serve as aids for plants to attract more pollinators than other flowers.

In autumn large flowers serve as "discovery advertisement". The flowers are used as sign posts to be detected by the pollinator from a distance. The low nectar quantities of *Colchicum* spp., *Crocus* spp., and *Sternbergia clusiana* (Shmida and Dafni, unpublished) reflect "oligopolistic market"(Selten 1983a, b; Friedman 1979) in which competition is poor. Thus, the low reward indirectly indicates that the large flowers serve as a means of "discovery advertisement" and not as a competitive one. In a competitive market one may expect a monotonic relation between investment in reward and in advertisement, meaning that large flowers gain a higher reward (Milgrom and Roberts 1986; Shmida and Cohen 1989; Tirole 1988). The same basic model holds to explain the flowers morphology of *Allium* in late spring-early summer. These species have very small, inconspicuous, low rewarding flowers which correspond to a market of "sellers"

Colors in the "Lily Group" Species

The white color is prominent in the winter flowering "Lily-group" species, 47% of which flower in December-January and 52% in February. There are several possible explanations as to why white flowers are advantageous. Among these, species of *Ornithogalum* and *Allium* are notable as having UV high color (Shmida and Menzel 1989). It has been argued (Kevan 1983; Faegri and Van der Pijl 1979) that night pollinated flowers, especially those pollinated by hawkmoths, are frequently white. However, in Israel the winters are too cold for the activity of these insects (Yathom and Rivnay 1967) and thus, those insects are almost absent in this season.

White flowers may attract heat in cold weather (Kevan 1972) and may serve as heat shelters. Although some white flowers of the "Lily-group" are bell-shaped and closed at night (e.g., *Crocus hyemalis*) sleeping insects are rarely found inside them. White coloration of flowers is regarded as advantageous under poor light conditions, especially when under a tree canopy in woods (Schemske *et al*. 1980; Baker and Hurd 1968; Dafni 1989). In Israel the "Lily-group" white species usually appear in open and well-illuminated habitats.

We tend to consider the advantage of white color in a season of poor color diversity, as serving as a contrast to the dark general background. In the Mediterranean territory the "Lily-group" species commonly appear on dark bare soils (e.g., basalt and grumosol) before the rainy season on a dark green background of the new seedlings carpet during the winter.

Analysis of the colors in the "Lily-group" indicates (Table 3) a relatively high frequency of the pink, purple, and blue flowers over yellow ones. There is increasing evidence that pink-purple flowers are favored by large highly rewarded insects with long mouth-parts, while yellow flowers attract smaller low-rewarded ones having shorter mouth-parts (Shmida and Dukas 1989; Willemstein 1987; Rebelo *et al*. 1985; Heinrich 1983; Dukas and Shmida 1989).

Floral size in relation to plant height

Primack (1987) argues that bigger plants produce bigger flowers and attract larger pollinators. Our results (Table 4) show the opposite direction and show a significant negative correlation ($r = 0.62$; $p = 0.05$) between size and height. The pollinators of *Sternbergia clusiana*, which has large flowers (up to 8cm) are small solitary bees and syrphids (Dafni and Werker 1982). These are similar in size to the pollinators of *Pancratium parviflorum* (flower size 3-4cm) and *Colchicum steveni* (flower size 3-4cm). *Colchicum stereni* shares some of the solitary bees which also pollinate *Scilla autumnalis* (flower size 3-4mm) (Dafni, unpublished). These data do not corroborate the general trend outlined by Primack (1987) who suggested that the large flowers are pollinated by large pollinators. Our results reflect local conditions which are dominated by the seasonal pollination market regardless of plant height. We explain the discrepancy between the flower size and the plant height and/or the pollinator's size as a result of the increasing height of the general plant canopy from the winter throughout the summer (Novoplansky, pers. comm.). The highest "Lily-group" species (excluding *Lilium candidum*) are summer *Allium* species bearing small flowers above the herbs' canopy.

Therefore, in the summer there is a shift in the "pollination market" from a shortage of flowers to a shortage of insects and, thus, flowers that bear long stalks above the plant canopy may have more chances to be detected.

In the autumn all the herbaceous vegetation is dry and the soil is bare. Accordingly, the flowers grow close to the soil's surface (several centimeters) and there is no evidence of any selective pressure to produce organs to elevate the flowers. We think that under the local conditions, there is no connection between the plant height and the flower size, in the flora of

Israel as well as in the "Lily-group" geophytes (Table 4). These factors are related to the "pollination market" situation (Shmida and Cohen 1989). Two species of the "Lily-group" are exceptional—*Urginea maritima* flowers from August to October on a high (flowering stalk (up to 1.5m). this phenomenon could be due to the prevailing of partial wind pollination in this species (Dafni and Dukas 1986). *Pancratium maritimum* sits on high flowering stalks (up to 0.5m) and flowers near seashores on moving sand (Eisikowitch 1981). The elevated position of the flower may serve to reduce the harm of the abrasive, mobile sand.

Stylized Morphological Patterns within the "Lily Group" Species

Although the "Lily-group" species show high diversification in flower form as well as in size, many species may be grouped together by the "stylized morphological patterns" that they exhibit:

a) Small open flowers with no protection of nectar, flowering early (August-November), before the rainy season, e.g., *Scilla autumnalis, S. hanburyi, Urginea maritima* and *U. undulata*, the pollinators are generalists small bees and flies.
b) Big campanulate-funnel-shaped flowers with a low quantity of exposed nectar and pollen offered to a large spectrum of unspecialized pollinators. The flowering is during October to December, e.g., *Colchicum* spp.and *Crocus* spp.
c) "Rain flowers"—closed or reverse flowers which are protected from rain (*Hyacinthus, Muscari* and *Narcissus*). These flowers have a special structure or a spatial position to protect the nectar from dilution as well as from damage.
d) Early spring" flowers—these showing a high diversification, adaptation of various pollinators, especially to long-tongued bees and bombylids (e.g., *Bellevalia* spp.).
e) Summer flowers—of all the "Lily-group" species, only *Allium* species peak in this season. The flowers are small, dull colored, closed, and held on high flowering stalks. The inflorescence is a dense umbel which is convergent to that of the Umbelliferae and the Compositae which are dominant in this season. The common pollinators are short-tongued, solitary bees and flies.
f) Open flowers with protected nectar. In the flowers of *Asphodelus* species and *Ornithogalum* species there is free access to the pollen, the nectar, however, is concealed by the broad base of the filaments. The nectar is semi-protected from rain damage and can be reached only by long-tongued pollinators.

In conclusion, the "Lily-group" geophytes comprise a special ecological group in the flora of Israel. They have large flowers and two peaks of blooming, one in the spring and one in the autumn. The flower size and reward changes during the year are explained in terms of "competitive" and "discovery" advertisement, which are molded by the prevailing "pollination market" in each season.

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LITERATURE CITED

Auerbach, M. and A. Shmida 1987. Spatial scale and the determinants of plant species richness. **Trends in Ecology and Evolution** 2:238-242.

Baker, H.G., and P.D. Hurd 1968. Intrafloral ecology. **Annual Review of Entomology** 13:385-414.

Burtt, B.L. 1970. The evolution and taxonomic significance of a subterranean ovary in certain monocotyledons. **Israel Journal of Botany** 19:77-90.

Dafni, A. 1989. The geophytes of Israel—distribution, ecology and reproductive cycles. Proc. OPTIMA 5th Meeting (Istanbul, Sept. 1986) (In Press).

Dafni, A., P. Bernhardt, A. Shmida, Y. Ivri, S. Greenbaum, C. O'Toole and L. Losito 1990. Red bowl-shaped flowers—convergence in the Mediterranean and beetle pollination. In: **Advances in Pollination Ecology,** A. Dafni and D. Eisikowitch (eds.), The Weizmann Science Press of Israel, Jerusalem, pp. 81–92..

Dafni, A., D. Cohen and F. Noy-Meir. 1981a. Life-cycle variation in geophytes. **Annals Mo. Bot. Gard.** 68:652-660.

Dafni, A. and R. Dukas 1986. Insect and wind pollination in *Urginea maritima* (Liliaceae). **Plant Systematics and Evolution** 154:1-10.

Dafni, A. and A. Shmida 1989. Flower colors and blooming phenology in the flora of Israel (MS).

Dafni, A., A. Shmida and M. Avishai 1981b. Leafless autumnal-flowering geophytes in the Mediterranean region—phytogeographical, ecological and evolutionary aspects. **Plant Systematics and Evolution** 137:181-193.

Dafni, A. and E. Werker 1982. Pollination ecology of *Sternbergia clusiana* (Ker-Gawler) Spreng, (Amaryllidaceae). **New Phytologist** 91:571-577.

Dahlgren, R.M.T., Clifford, H.T. and P.F. Yeo 1985. **The families of the monocotyleds: Structure, evolution and taxonomy.** 520 pp. Springer-Verlag. Berlin.

Dukas, R. and A. Shmida 1989. Correlation between the color, size, and shape of crucifer flowers and relationships to pollinators. **Oikos** 54:281-286.

Eisikowitch, D. 1971. Effect of wind on the pollination of *Pancratium maritimum* L. (Amaryllidaceae) by hawkmoths (Lepidoptera: Sphingidae). **Journ. Animal Ecology** 40:673-678.

Evanari, M., and Y. Gutterman 1985. Desert plants. pp. 45-53.in: **Handbook of Flowering.** Vol. I, A. Halevy (ed.), C.R.C., Florida, U.S.A.

Faegri, K. and L. Van der Pijl 1979. The Principles of Pollination Ecology, 3rd ed. Pergamon Press, Oxford, 244pp.

Friedman. J.W. 1977. Oligopoly and the Theory of Games. 311 pp. North-Holland Pub., Amsterdam.

Heinrich, B. 1983. Insect foraging energetics. p. 187-214. In: Handbook of Experimental Pollination Biology. Jones, C. E. and R.J. Little (eds.), Scientific and Academic Editions, New York. 558pp.

Holdsworth, M. 1961. The flowering of rain flowers. **Journ. West Afr. Sci. Assn.** 7:28-36.

Kevan, P.G. 1972. Floral colors in the high Arctic with reference to insect flower relations and pollination. **Canadian Journ. Botany** 50:2289-2316.

_____ 1983. Floral colors through the insect eye: what they are and what they mean. pp. 3-30, in: Handbook of Experimental Pollination Ecology. Jones, C.E. and R.J. Little (eds.)., Scientific and Academic Editions, New York, 558pp.

Mathew, B. 1987. The Smaller Bulbs. Batsford, London 190 pp.

Mathew, B. and T. Baytop 1984. The Bulbous Plants of Turkey. Batsford, London. 132 pp.

Milgrom, P. and J. Roberts 1985. Price and advertising signals of product quality. Research Paper No. 742. Stanford University Press.

Mooney, H.A. and W.D. Billings 1960. The annual carbohydrate cycle of alpine plants as related to growth. **Amer. Journ. Botany** 47:594-598.

_____ 1961. Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna* **Journal of Ecology** 62:291-324.

Pate, J.S. and R.W. Dixon 1982. Plants with fleshy underground storage organs—a western Australian view. pp. 181-215. In: Biology of Australian Plants. J.S. Pate and A.J. McComb (eds.), University of Western Australia Press, Perth, Australia.

Primack, F.B., 1987. Relationship among flowers, fruits and seeds. **Ann. Rev. Ecology Syst.** 18:403-430.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. pp. 305-329 in: Pollination Biology, L. Real (ed.), Academic Press, Harcourt Brace Jovanovich, Publishers, Orlando.

Rebelo, A.G., W. R. Siegfried and E. G. H. Oliver 1985. Pollination syndromes of *Erica* species in the southern Cape. **South African Journnal of Botany** 52:270-280.

Rees, A.R. 1972. The Growth of Bulbs. Academic Press, London & New York, 291 p.

Schemske, D.W., M.F. Wilson, M.N. Melampy, L.J. Miller, L. Verner, K.M. Schemske and L.B. Best. 1978. Flowering ecology of some spring woodland herbs. **Ecology** 53:351-366.

Selten, R. 1983a. Evolutionary stability in extensive two-person games. **Mathematical and Sociological Sciences** 5:269-283.

_____ 1983b. A model of oligopolistic size structure and profitability. **European Economical Research** 22:33-57.

Selten, R. and A. Shmida 1989. Pollinator foraging and flower competition in a game equilibrium model. In: R. Selten (ed.) Game Theory in Behavioral Sciences (in press).

Shmida, A. 1981. Mediterranean vegetation of Israel and California, similarities and differences. **Israel Journnal of Botany** 30(3):105-123.

Shmida, A. and T. Burgess 1988. Plant Growth-Form Strategies and Vegetation Types in Arid Environments. In: M.J. Werger (ed.), Vegetation Structure. The Hague, Netherlands, pp. 1-31.

Shmida, A. and D. Cohen 1989. The evolution of flower display and reward (Mimeo).

Shmida, A. and R. Dukas 1986. Abundance of insects and pollinators in *Har Gilo*, Jerusalem region: Primary obse vations. **Rotem.** 21:19-26 (Hebrew, English summary).

_____ 1989. Interactions of pollinating insects with flowers in a Mediterranean community. **Oecologia** (in pre

_____ 1989. Reduction is sizes of solitary bees during the flowering season and its correlation to the sizes bee flowers of the Mint family (Lamiaceae), **Israel Journal of Botany**, 39:133-142.

Shmida, A. and R. Menzel 1989. Ecological aspects of flowers with UV reflection in relation to insect pollinators (MS

Shmida, A. and S. Ritman 1985. The Israel plant data-base: unified approach to ecology, phytogeography, floristi teaching, and conservation. pp. 91-95 in: The Role of Data in Scientific Progress, P.S. Glaeser (ed.), Elsevi Science Publishers, B.V. North Holland.

Strid, A. 1987. Some autumn-flowering bulbs of Greece. **Herbertia** 43:12-21.

Svoskin, I.P. 1960. Specific biological characteristics of bulbous geophytes as related to their past and present ecolog **Botanicky Zhurnal** 45:1073-1078.

Tirole, J. 1988. The theory of industrial organization. 479 pp. M.I.T. Press, Cambridge, Mass.

Waser, N.M. 1986. Flower constancy: definition, cause and measurement. **American Naturalist** 127:593-603.

Willemstein, S.C. 1987. An evolutionary basis for pollination ecology. E.J. Brill. Leiden University Press. Leide 425 pp.

Yathom, Sh. and E. Rivnay 1967. Phenology of hawkmoth species in Israel. **Ktavim** 17:57-72 (In Hebrew).

Zohary, M. 1962. Plant life in Palestine. Ronald Press, New York.

Zohary, M. and N. Feinbrun-Dothan 1966-1984. Flora Palaestina. Vols. 1-4. Israel Academy of Sciences and Humanitie

IRIS, SUBGENUS *HERMODACTYLOIDES* OR THE RETICULATA IRISES

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ALTHOUGH this popular group of small Western and Central Asiatic spring-flowering bulbous irises is usually known as the Reticulata Section following the classification of W.R. Dykes (1913), it is clear that they are sufficiently distinct to merit a much higher taxonomic status than that of a Section. In fact, the Soviet Iris authority G.I. Rodionenko (1961), has gone so far as to suggest that there are several genera housed within the broad concept of *Iris* and he recognised several 'splits' including *Juno* and *Iridodictyum*, the latter encompassing all those species previously known as the Reticulata Section. It is my opinion that this constitutes an excessive degree of splitting since it appears that there are certain links between this 'Reticulata' group of species and the rhizomatous irises of subgenus *Limniris*, series *Syriacae* (Diels) Lawrence. If a separate genus represents too high a status for "Reticulata", and Section too low, then the obvious level of recognition to adopt is that of subgenus, which is exactly where Spach placed *I. reticulata* in 1846. Although at that time it was the only known species, the classification has stood up well and 9 other species have been added to what appears to be a fairly natural group. The correct name at subgeneric level is *Hermodactyloides* Spach, a cumbersome epithet referring to the fact that the leaves of *I. reticulata* have a squarish cross-sectional shape similar to those of *Hermodactylus tuberosus* (*Iris tuberosa*). Although I have little doubt that this is the correct classification of the group, I have also no doubts at all that these familiar little irises will continue to be called 'the Reticulatas'!

Above, I refer to the group as being 'fairly natural' and this comment should therefore be explained. Most of the 10 species do form a convincing assemblage based on several characteristics, but the two outlying species in Soviet Central Asia, i.e., *I. kolpakowskiana* and *I. winkleri*, do not entirely confirm particularly on account of their channelled leaves which are more like those of an *Iris* of subgenus *Scorpiris* (syn. section *Juno*) or perhaps even a *Crocus*. Cytology, at the superficial level of chromosomes counts, does not appear to help since *I. kolpakowskiana*, the Central Asiatic 'Juno' irises, such as *I. nicolai* and *I. rosenbachiana*, and the Central Asiatic crocuses, *C. alatavicus* and *C. korolkowii*, all have a chromosome number of $2n = 20$. However, it is possible that more detailed studies of the karyotype would reveal significant differences in the chromosome morphology but as yet such studies have not been undertaken. Pollen studies at Kew, however, indicate that there are no close relationships between *I. kolpakowskiana*, *Crocus* and *Iris* subgenus *Scorpiris*. Although they do not fit readily into the same group as the rest of the Reticulate Iris species, *I. kolpakowskiana* and *I. winkleri* are, for convenience at least, better placed here than anywhere else, but in their own section, which Rodionenko named *Monolepis* (in the genus *Iridodictyum*) on account of the single sheathing leaf which encloses the aerial shoot; in all other species there are several sheaths.

Although the rest of the species cluster together more readily, there are two which are distinct enough to also merit sections of their own. The well-known *I. danfordiae* is morphologically different from all other species in having reduced inner perianth segments which are like small bristles, and its chromosome number is also unique ($2n = 18$) in the group. The section name, *Micropogon*, was given by J.G. Baker in 1876, although in his classification as a subgenus of genus *Xiphion*; the name *Micropogon* refers to minute papillae on the claw of the falls. *I. pamphylica* is unique in being the only species to elevate its flowers to well above ground level on a scape rather than by means of an extra long perianth tube; in fact its perianth tube is much shorter than those of other species so that I have given the section to which it belongs the name *Brevituba*. The remaining six species (*I. reticulata*, *I. bakeriana*, *I. vartanii*, *I. histrio*, *I. histrioides* and *I. winogradowii*) are fairly uniform in their morphological characteristics but there is some variation in chromosome number, *I. histrioides* and *I. winogradowii* differing from the other four in having a diploid number of $2n = 16$ (*I. reticulata* and its immediate allies, $2n = 20$). This cytological difference in itself is not considered to make a strong enough case for splitting off *I. histrioides* and *I. winogradowii* into a separate section and they are accordingly placed with *I. reticulata*, the type species of the subgenus *Hermodactyloides*, in section *Hermodactyloides*.

To summarise, the classification of *Iris* subgenus *Hermodactyloides* is as follows:

Sect. **HERMODACTYLOIDES**
- *I. reticulata* M. Bieb.
- *I. bakeriana* Foster
- *I. vartanii* Foster
- *I. histrio* Reichb. fil.
- *I. histrioides* (G.F. Wilson) Arnott
- *I. winogradowii* Fomin

Sect. **BREVITUBA** B. Mathew
- *I. pamphylica* Hedge

Sect. **MICROPOGON** (Baker) Boiss.
- *I. danfordiae* (Baker) Boiss.

Sect. **MONOLEPIS** (Rodion.) B. Mathew
- *I. kolpakowskiana* Regel
- *I. winkleri* Regel

KEY TO THE SECTIONS

1a. Aerial shoot enclosed within 1 sheathing leaf; leaves channelled; stigma flap, entire leaves (4) sect. *Monolepis*

b. Aerial shoot enclosed within 2 or more sheathing leaves 4-angled or cylindrical; stigma flap bilobed 2

2a. Stem produced well above ground (at least 10cm); perianth tube rather short (ca. 2cm); capsule pendent at maturity (3) sect. *Brevituba*

b. Stem subterranean; perianth tube at least 3cm long; capsule erect 3

3a. Inner perianth segments (standards) much reduced, bristle-like and insignificant (2) sect. *Micropogon*

b. Inner perianth segments not greatly reduced and forming significant erect 'standards' (1) sect. *Hermodactyloides*

PRACTICAL KEY TO IDENTIFICATION OF SPECIES

1a. Flowers yellow 2
b. Flowers blue, purple, violet (rarely white) 3
2a. Inner segments (standards) greatly reduced and inconspicuous ..... 10. *I. danfordiae*
b. Inner segments not greatly reduced and conspicuous ..... 9. *I. winogradowii*
3a. Stem well-developed above ground; perianth tube only ca. 2cm long ..... 1. *I. pamphylica*
b. Stem below ground; perianth tube 3cm or more long 4
4a. Leaves channelled 5
b. Leaves 4-angled or terete 6
5a. Bulb tunics netted-fibrous ..... 2. *I. kolpakowskiana*
b. Bulb tunics papery ..... 3. *I. winkleri*
6a. Lobes of style branches 2-2.5cm long, narrowly acuminate ..... b. *I. vartanii*
b. Lobes of style branches usually less than 2cm long and obtuse or acute 7
7a. Leaves almost terete in section with 8 ribs ..... 5. *I. bakeriana*
b. Leaves 4-angled in cross section 8
8a. Bract and bracteole green, rather rigid and closely sheathing the perianth tube . 4. *I. reticulata*
b. Bract and bracteole thin and membranous, whitish or sometimes faintly tinged green 9
9a. Falls spotted dark blue on a pale ground in the central part of the lamina only ..... 8. *I. histrioides*
b. Falls blotched blue on a whitish or pale blue ground over most of the area of the lamina 7. *I. histrio*

1. *I. pamphylica* Hedge in Notes R.B.G. Edinb. 23: 557 (1961). Type: Turkey, Antalya Province, Manavgat to Akseki, *Davis & O. Polunin* 25845 (holo. E; iso. K).

I. pamphylica takes its name from the ancient region of Pamphylia in southern Turkey where it is known from only one locality and may well be nearing extinction in that site (B. Mathew per. obs.). Within subgenus *Hermodactyloides* it is very distinct in having an aerial stem holding the flowers well above ground level rather than on a very long perianth tube with a subterranean stem as in all other species; in the fruiting state its capsules are held in a dangling position on the 15-20cm stems, whereas in other species they are carried erect at ground level. The flower colours are a curious mixture of colours: the falls have a deep brownish-purple lamina with a yellow median ridge which is spotted purple, while the claw of the falls is green with darker spots; the standards are blue-veined,darker, shading to green at the base. Although the bulb is apparently similar to that of the other species it has a few interesting differences such as rather thick fleshy roots and some small needle-like fibres at its base; these features suggest a link with the *Iris* species of series *Syriaceae* and notably *I. masia* from Southern Turkey which possesses bulbs of a similar structure, although larger. Pollen studies at Kew suggest that there is a relationship between these groups, since *I. pamphylica* has a pollen structure similar to that of *I. masia* and rather different from that of the species in section *Hermodactyloides* (i.e., *I. reticulata, et al.*). *I. pamphylica* does however have 4-angled leaves which resemble those of *I. reticulata* and its allies rather than *I. masia* which has flat, narrowly ensiform, leaves. On the other hand, Arber (1921) did not consider that the 4-angled leaf shape was greatly different and stated that it was merely a variant of the ensiform type. All this suggests that *I. pamphylica* of subgenus *Hermodactyloides* and *I. masia* of series *Syriacae* might at least share a common ancestry which in turn indicates a link with the rhizomatous beardless irises of subgenus *Limniris*.

2. *I. kolpakowskiana* Regel in Acta Hort. Petrop. 5: 263 (1877). Type: USSR, Kazakh S.S.R. near Alma-Ata, *Fetisow* (holo. LE; iso, K).

This distinctive little Iris has lilac or violet flowers with a darker violet lamina to the falls which have a yellow median ridge. Unlike all other species, except *I. winkleri*, the aerial shoot is enclosed within one cataphyll (sheathing leaf), and it is also unique (although *I. winkleri* is probably the same) in having an entire, not bilobed, stigma flap. In its pollen morphology it is unlike the species of other sections and the leaves have a deep channel on the upper surface and a whitish median stripe, whereas most of the Reticulata irises have leaves with a quadrangular section. Even in the fruiting stage it is distinct on account of the cylindrical capsule, and the seeds do not possess an appendage as do the other species. Nevertheless, it and *I. winkleri* are probably better housed within subgenus *Hermodactyloides* than in the other bulbous group, subgenus *Scorpiris*, although it does have a few features in common with the latter. Rodionenko (1961) has suggested that in view of certain of its features it may have evolved from an ancient cross between an Iris of subgenus *Hermodactyloides* and a *Crocus*. Possibly, however, a better scenario for its origin would involve the ancestral stocks of subgenus *Scorpiris* and the genus *Crocus*. Chromosome counts may be of significance here in that the sympatric species *I. kolpakowskiana*, *I. rosenbachiana* (subgenus *Scorpiris*) and *Crocus alatavicus* all have a diploid number of $2n = 20$.

3. *I. winkleri* Regel in Acta Hort. Petrop. 8: 677 (1884). Type: USSR, Kirgiz S.S.R., between Urgent and Alabuga, *A. Regel* (holo. LE).

This little-known species may, in fact be based on an aberrant specimen of *I. kolpakowskiana*. The one collection from the 19th century was described as a new species on account of the fact that the bulb tunics were membranous, not reticulate-fibrous as in *I. kolpakowskiana*; otherwise the two appear to be much the same in their characters. It is possible that the specimen is merely a plant of *I. kolpakowskiana* which has lost its outer fibrous bulb tunics. Searches have been made in the area but *I. winkleri* has not been rediscovered.

4. *I. reticulata* M. Bieb., Fl. Taur.-Cauc.: 34 (1808). Type: USSR, Caucasus "Iberia", without a precise locality, *Adam* (holo. LE)

This, the type species of the subgenus, is the most widespread and variable of all the Reticulata irises, exhibiting in the wild a great range of flower colours in the blue, violet and purple shades. There is also variation in the degree of coarseness of the bulb tunic, and in the extent to which bulblets are produced, some having many small 'rice grains' surrounding the parent bulb while others produce few or none. The name, *I. hyrcana* Woron., has been attached to a pale, clear blue form from the Caspian region and this has, by vegetative propagation, recently become fairly readily available in commerce. However, in the wild this is not uniform and it is possible to find purple and blue forms intermixed. The characters used to distinguish *I. hyrcana*, namely the globose shape of the bulb and the large number of bulblets produced, are not very convincing taxonomically since these features vary considerably with *I. reticulata*. Nevertheless, this variant from the Hyrcanian area of the Caspian is horticulturally distinct and requires a distinguishing name, if only for commercial purposes.

A plant cultivated as *I. sophenensis* should probably also be regarded as a variant of *I. reticulata*. It has deep violet-blue flowers with rather narrow perianth segments.

I. reticulata is widespread in eastern Turkey, the Caucasus, north and west Iran and northern Iraq. In cultivation many forms have been selected and named, from white ('Alba') to pale

blue ('Natasha', 'Cantab') to deeper blue ('Joyce', 'Harmony') and deep purple ('J.S. Dijt', 'Krelagei') or violet ('Violet Beauty'). Some cultivars are hybrids with *I. bakeriana* showing intermediate leaves with a variable number of ribs, but usually 6, while others appear to be derived from crosses with *I. histrioides*. It should be possible to detect the presence of the latter in a hybrid since it has a different chromosome number ($2n = 16$) from *I. reticulata* ($2n = 20$).

Undoubtedly *I. reticulata* is the most 'difficult' species taxonomically speaking. It seems unsatisfactory to treat it in a broad sense, encompassing many very different-looking plants, but on the other hand there does not seem to be a sound basis for dividing it into several taxa.

5. *I. bakeriana* Foster in Bot. Mag. 115: t. 7084 (1889). Type: Turkey, Mardin 1887, *Rev. G.F. Gates* (holo. K).

This differs markedly from *I. reticulata* in the cross-sectional shape of its leaves which are almost cylindrical with 8 ribs or veins, thus appearing quite different from the 4-angled ones of most other species. The flowers, in the Turkish form which is the one most frequently seen, are pale blue with a dark lamina to the falls, which lack a yellow median ridge. However, I have seen forms in Iran which have a bright yellow ridge but lack the conspicuously darker lamina. *I. bakeriana* is much more restricted in its distribution and occurs only in extreme Southeastern Turkey, Northeastern Iraq and Western Iran. It hybridises with *I. reticulata* and the resulting cultivars often have 6 ribs in the leaves.

6. *I. vartanii* Foster in Gard. Chron. 1885: 438 (1885). Type: Israel, cultivated in Britain by M. Foster in 1884 from bulbs sent by *Dr. Vartan*.

I. vartanii is seldom seen in cultivation but is a most attractive species with flowers of a clear pale slatey-blue, or rarely white. The most distinctive feature concerns the lobes of the style branches which are long and narrowly acuminate, but the colour also makes it fairly easily distinguishable from all other species; there is almost none of the spotting on the falls which is such a notable characteristic of sympatric *I. histrio*. *I. vartanii* is a plant of open rocky places and scrub in Israel, Lebanon, Southern Syria and Northwestern Jordan.

7. *I. histrio* Reichb. fil. in Bot. Zeit. 30: 488 (1872). Type: Lebanon, summit of Lebanon Mts. near Saida, *Gaillardot* (iso. K).

There are two subspecies of *I. histrio*: ssp. *histrio* has large flowers with the falls 1.2-1.6cm wide (across the widest part of the lamina) which is pale blue and conspicuously blotched dark blue over much of the surface; this has a fairly wide distribution from Southern Turkey south through Syria and Lebanon to Israel. Subsp. *aintabensis* (G.P. Baker) B. Mathew has smaller flowers in which the lamina is only 0.8-1.1cm wide and the darker blue blotches are clustered towards the centre of the lamina. The type specimen comes from the region of Gaziantep (previously Aintab) in southern Turkey and it has been found in several localities in the same general area. Both subspecies produce small rice-grain bulblets so that they could be increased quite rapidly for commercial purposes although curiously both are rare in cultivation.

8. *I. histrioides* (G.F. Wilson) Arnott in Journ. Hort. ser. 3, 24: 121, f. 18 (1892). Type: Turkey, grown by G.F. Wilson from bulbs obtained from the German nursery of Max Leichtlin.

Although *I. histrioides* bears some resemblance to *I. histrio* it is not difficult to distinguish the two species in the living state on account of the colour and markings. *I. histrioides* is a deeper blue throughout and although the falls are blotched darker, the markings are aggregated towards the centre of the lamina. There is also a subtle difference in the outline shape of the falls although this can only be seen clearly when a fall is removed from the flower and flattened out. Then it can be seen that in *I. histrioides* there is a distinctly narrower part between the lamina and the claw whereas the falls of *I. histrio* merge from the lamina to the claw with no obvious notch separating them. The two differ in chromosome number, *I. histrio* having a count of $2n = 20$ and *I. histrioides*, $2n = 16$.

I. histrioides is a very local species, occurring only in northern Turkey where it was until recently known only in the region around Amasya. However, it has now been located farther to the east in Rize province.

In cultivation there are now several variants of *I. histrioides* differing only slightly in the depth of the blue background colour, except for one colour break which is a deep rich purple. This (cv. 'George') may well be a hybrid with one of the purple forms of *I. reticulata*, although morphologically it is very similar to *I. histrioides*. The most commonly seen cultivar of *I. histrioides* is 'Major', a plant introduced by the Dutch firm of van Tubergen in the early part of the 20th century from a Turkish collection by J.J. Manissadjian. Interestingly, the name 'Major' was given to it, not because it was larger than other individuals of *I. histrioides*, but to distinguish it from a smaller flowered Iris which was known from the south of Turkey and also thought to represent *I. histrioides*, although it was most likely a form of *I. reticulata* or *I. histrio*. Recent wild collections in Turkey from the Amasya region show that 'Major' is in fact fairly typical in its size and colour for the species. Unfortunately, nursery stocks have become somewhat confused and there is now more than one form in cultivation under the name 'Major'.

9. *I. winogradowii* Fomin in Woron. & Schelk., Sched. Herb. Fl. Cauc. No. 166 (1914). Type: USSR, Transcaucasia, Mt. Lomis-Mta. 28 April 1913, *Mlokosiewicz* (holo. LE).

This yellow-flowered species is closely allied to *I. histrioides* and shares with it the same chromosome number $2n = 16$; consequently, it is not surprising that the two will hybridise to give pale yellowish-blue intermediates (e.g., cv. 'Katharine Hodgkin'). Although in the bearded Iris species (i.e., subgenus *Iris*, section *Iris*), blue or purple and yellow forms frequently occur in mixed populations, this does not happen in subgenus *Hermodactyloides* and it is clear that the blue *I. histrioides* and the yellow *I. winogradowii* should be regarded as separate taxa. Apart from the distinguishing colours there is a difference between the two species in the shape and size of the style branches: in *I. winogradowii* they are oblanceolate and 0.6-1.1cm wide, whilst in *I. histrioides* they are markedly wedge-shaped and 1.3-1.6cm wide at the widest point at the base of the two lobes.

Although a very rare plant in the wild (a few hundred plants only according to Dr. G. Rodionenko), *I. winogradowii* increases quite well in cultivation and is fairly readily obtainable. It is known only from the type locality in the Caucasus.

10. *I. danfordiae* (Baker) Boiss., Fl. Orient. 5: 124 (1882). Type: Turkey, Adana Prov., Cilician Taurus, near Anascha, 24 March 1876, *Mrs. Danford* (holo. K).

This is a very distinctive species on account of the yellow flowers and reduced standards which are represented by no more than bristle-like appendages between the falls. It has a different chromosome number from all others ($2n$=18) and has not, to my knowledge, been successfully hybridised with any other. Reports of crosses have been made from time to time but none of these has been confirmed. The reason for lack of success might be that *I. danfordiae* is mainly represented in gardens by a sterile triploid ($3n = 27$) and this has very low pollen fertility; the diploid has not, until recently, been available for experimental hybridisation.

I. danfordiae is not a common plant in Turkey but has been recorded in several disjunct localities mainly in the eastern central part of Anatolia. The origin of the triploid cultivar, which is propagated each year in Holland in tens of thousands, is not known for certain. It was introduced by the firm of Van Tubergen and it seems likely that it was one of a batch of collected bulbs and, because of increased vigour, was the one which survived best under cultivated conditions; since it also increased well vegetatively it soon became commercially available. The diploid *I. danfordiae* is much less vigorous and has slightly smaller flowers.

HYBRIDS As mentioned above, there are many cultivars within subgenus **Hermodactyloides** and some of these are undoubtedly of hybrid origin.

Artificial hybrids exist between the following:

I. histrioides×*I. reticulata*
I. histrioides×*I. winogradowii*
I. bakeriana×*I. reticulata*

Early reports that *I. danfordiae* and *I. histrioides* were hybridised to produce 'Katharine Hodgkin' can be discounted. Cytological studies and morphological comparisons at Kew show that the parentage of this hybrid is undoubtedly *I. histrioides*×*I. winogradowii*.

Although there is already a good range of cultivars available, it could almost certainly be added to by the use of such species as *I. histrio*, *I. vartanii* and the diploid *I. danfordiae* in a breeding programme.

ASPECTS OF RESEARCH ON AMARYLLIDACEAE JAUME.

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TRAUB (1963) divided Amaryllidaceae into 4 subfamilies: Allioideae, Hemerocalloidae, Ixiolirioideae and Amarylloideae. They comprise 98 genera and 23 tribes. Dahlgren, Clifford and Yeo (1985), and later Takhtadjan (1987), excluded the first three subfamilies from Amaryllidaceae and so the number of tribes (Dahlgren—9, Takhtadjan—13) and species were also reduced. Such a size for the family Amaryllidaceae seems more natural in character.

In the last few decades, after a long interval of inactivity, the interest with amaryllids is growing again, particularly in America and Africa. Synonymy is being clarified, new genera and species are being described. In this connection some questions arise which are to be solved. To delimit the size of the family and resolve taxa synonymy of amaryllids, standardization of the description of new species is of great significance. It is also important to consider new features taken from living and herbarium specimens, otherwise some misunderstandings will take place. Consider the following example:

In the Botanical Register (1846) Misc. n. 63, a new species, *Hymenocallis harrisiana*, was described, from Mexico by Herbert. The same species was described by Baker (1881) in Botanical Magazine on t.6562. About a century later Traub (1967) described a new species, *Hymenocallis azteciana*, also from Mexico, and published a photo of this plant. Several years ago I got a few seed of *Hymenocallis harrisiana* from Amsterdam. When the plants flowered, I decided to verify the accuracy of the name. I was greatly surprised when, trying to find the picture of *H. harrisiana*, I came across the photo of *H. azteciana* and noticed the similarity of these species. Comparing their diagnoses I paid attention to the fact that they differed greatly, having just a few features in common. For example, 3-5 leaves divided into petiole and lamina, flowers 1-3 (6) in umbel; scape 20-23cm long, and the perianth is white. This led me to consider these species to be one and the same. An attempt to get some seeds or bulbs of these species from Mexico or the United States to compare them was not successful.

In describing the size of plant parts it is necessary to unify the units because different authors use various units (centimeter, inch, meter, foot, etc.).

Some additional difficulty is that of maps using old geographic names of the plant collection localities. Such names need to be cross-referenced with the new ones.

The use of living material while studying Amaryllidaceae of the USSR (Artyushenko 1970) proved to be very useful for resolving issues of taxonomy, phylogeny and evolution. Living, wild amaryllids were collected in "locus classicus" and grown in the nursery of Komarov Botanical Institute, Leningrad. It is useful and necessary to organize such collections in other countries where amaryllids grow natively and where specialists can research living specimens. This would help to study the different aspects of Amaryllidaceae.

In bulbous plants it is necessary to take into account the traditional features of aboveground organs, as well as the structure of underground organs, particularly the bulbs. This allows the possible clarification of some questions of taxonomy and the size of genera and tribes.

In studying Amaryllidaceae, data concerning ontogenesis are of great importance. The development of plants from seeds gives some new facts toward understanding more precisely the position of some taxa as well as many new data of the evolution of this family.

The important anatomical features of the leaf and scape are usually addressed quite insufficiently. It is rarely mentioned if the scape is solid or not. This feature is quite stable and useful in determining closely related taxa.

In the "Flora of the USSR" there are representatives of 5 genera of the family Amaryllidaceae: *Ungernia* Bunge, 7 species; *Leucojum* L., 2; *Galanthus* L., 11; *Sternbergia* Waldst. et Kit., 3; *Pancratium* L., 1; and *Narcissus* L., 1. As to the genus *Ixiolirion* Herb. with 5 species, it is now assigned to another family, the Ixioliridaceae Nakai.

Particular attention has been given to the development of such questions which, until now, have been out of the awareness of the majority of specialists. First of these is the structure of the bulb. While studying bulbous structure in detail some essential characteristics were determined, such as structure, quantity, and disposition of the lecus (basal plate) of the maturity fertile bulb.

BULB SCALES AND LEAVES NUMBERS

The scales arise either from lower leaves or from the basal part of the assimilative leaves. According to this feature not only genera but also species are distinguished. For example, the bulb of *Ungernia* annually forms 1-2 scales from the lower leaves and 2 from the assimilative leaves; *Galanthus*, 1 from lower leaves and 2 from assimilative leaves (Figure 1).

There are two types of scales: closed (concentric) and unclosed (imbricated). In *Ungernia* both types of scales are alternated and in *Galanthus* 2 scales are closed and 1 unclosed.

Leaf/scale capacity of a bulb is another important issue for consideration. In a growing bulb some scales die every year and new ones arise. Therefore, the scales grown during several years accumulate in the bulb. In our climate bulbous plants form new leaves according to the season of the year. During the spring new leaves are formed. After flowering they continue to grow until autumn and only during spring of the following year do they appear above the ground. Each new series of scales and leaves results in a scape. This limits the number of series of scales and leaves arising during several years.

Leaf/scale capacity of a bulb is a good parameter, not only for genera, but for species as well. In *Ungernia* there are 6 such series; in *Leucojum aestivum*, 3; in *L. vernum*, 2; in *Galanthus nivalis*, 2; in *G. caucasicus*, 3, 5, and so on. The structure of the bulb also relates to the character of its branching.

BRANCHING

There are two types of branching for bulbous plants, i.e. monopodial and sympodial. However, it is very difficult to find out the type of branching in bulbs because of their extremely short internodes. To define bulb branching a new method was elaborated (Artyushenko & Schepac 1982). This method is based on the position of scales before and after the scape and the character of phyllotaxy. Phyllotaxy of amaryllids is alternate or disticho-alternate (Fedorov, Kirpichnikov and Artyushenko 1962). If the scape is lateral, the apex of the shoot continues to develop leaves from year to year and the position of leaves does not change. This branching is called monopodial. In a case where the apex of the shoot is developed into a scape, its growth is finished and, instead, lateral shoot develop from the axis of the highest order. The phyllotaxy is disrupted and the scape is found between two leaves whose backsides are turned in one direction. In such case the branching is sympodial.

ANATOMICAL FEATURES

The epidermal structure is a stable feature to distinguish both genera and species. In *Galanthus* epidermal cells are elongated but in the European group they are constructed at

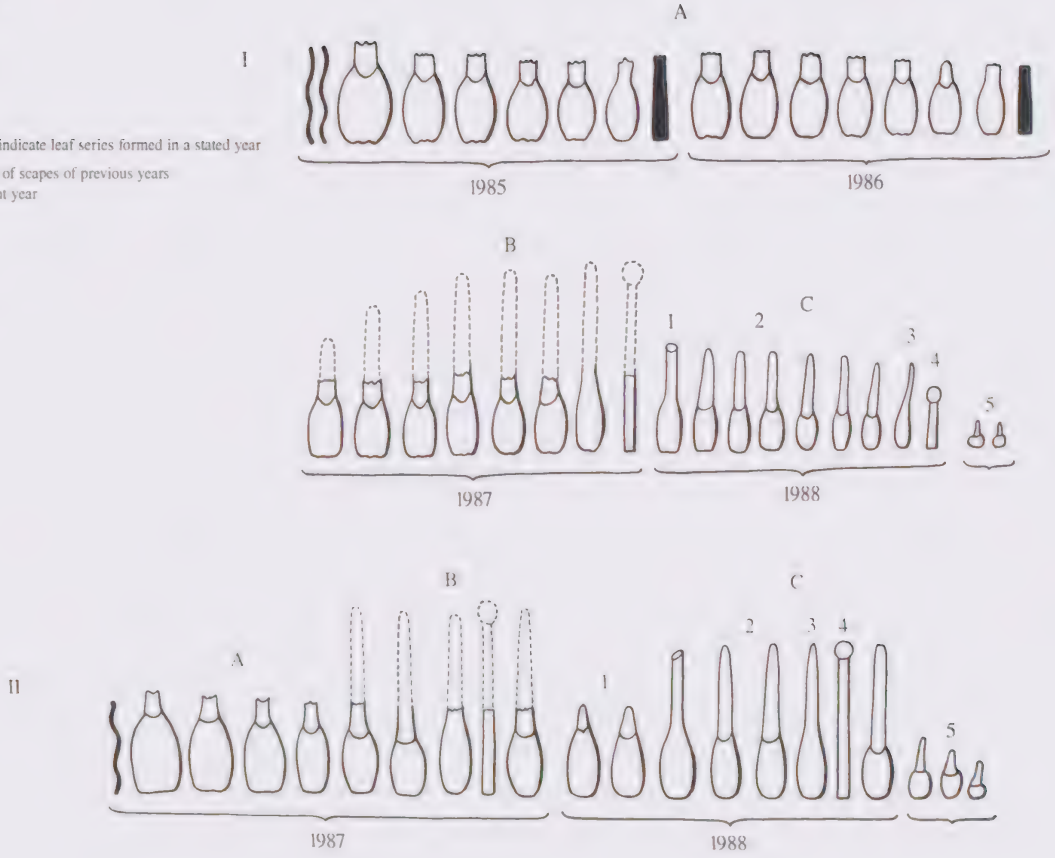
Figure 1. The structure of a bulb:

I. [illegible]
II. *Leucojum vernum*
III. *L. aestivum*
II. *Galanthus caucasicus*
V. G. *nivalis*.

The braces and dates under them indicate leaf series formed in a stated year

A — indicates scales and remains of scapes of previous years
B — indicates scales of the current year
C — a bud of next year

1—a scale with closed basis
2—a leaf with closed basis
3—a leaf with unclosed basis
4—a scape
5—young leaves



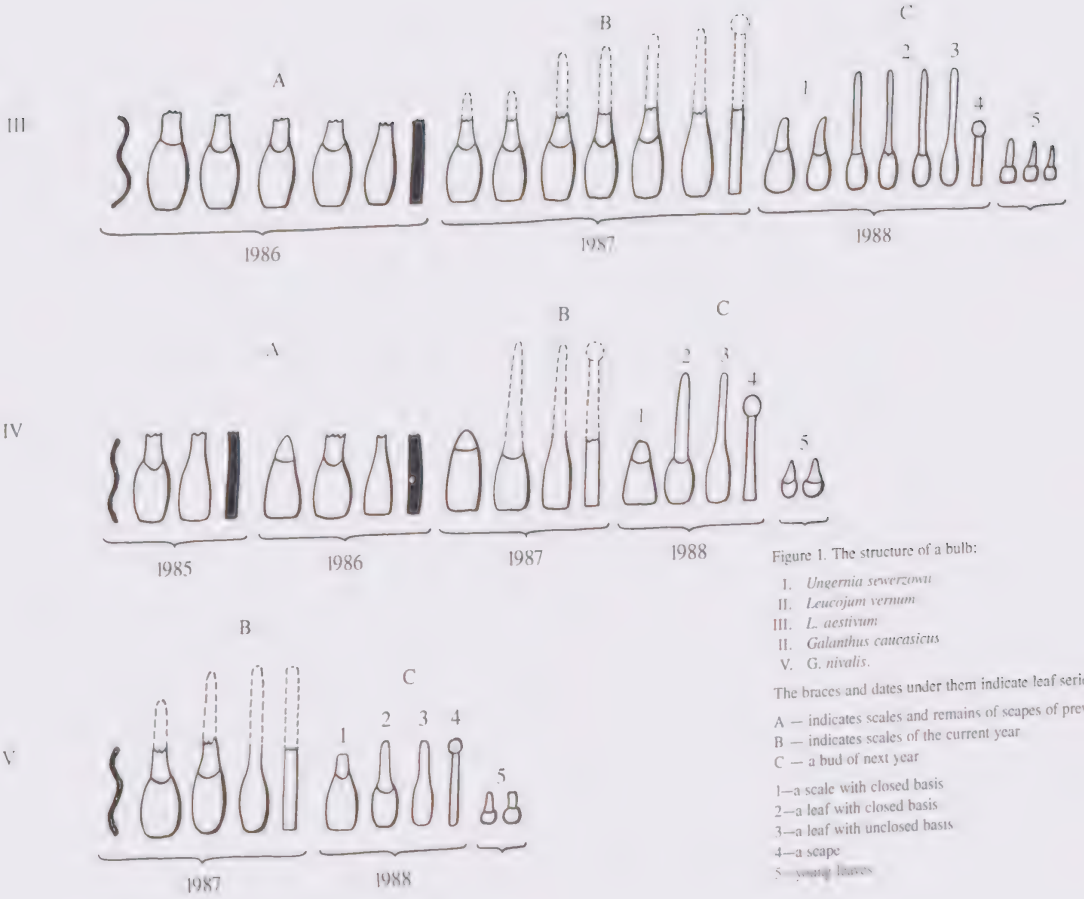


Figure 1. The structure of a bulb:

I. *Ungernia sewerzowii*
II. *Leucojum vernum*
III. *L. aestivum*
II. *Galanthus caucasicus*
V. *G. nivalis*.

The braces and dates under them indicate leaf series formed in a stated year

A — indicates scales and remains of scapes of previous years
B — indicates scales of the current year
C — a bud of next year

1—a scale with closed basis
2—a leaf with closed basis
3—a leaf with unclosed basis
4—a scape
5—young leaves

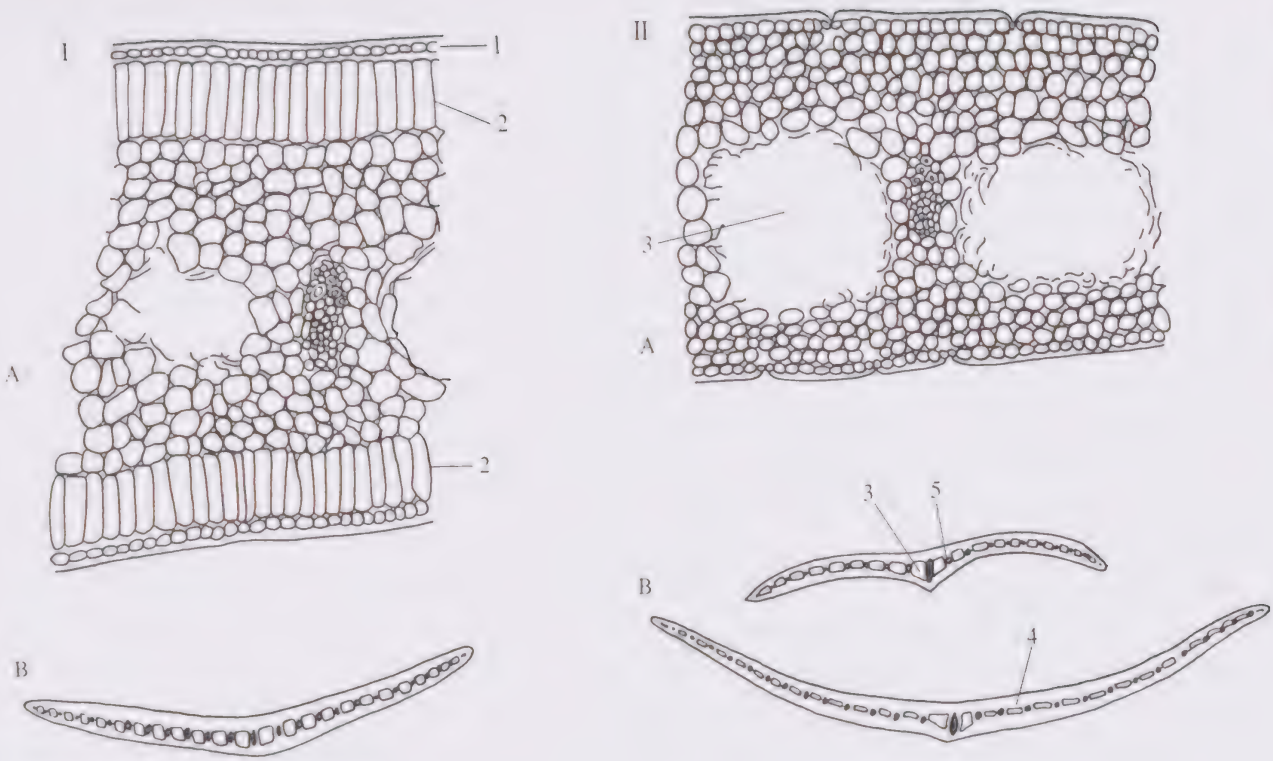


Figure 2. Anatomical structure of the leaves in cross section.

A—Indicates a part of the leaf
B—Indicates the whole leaf

I. *Ungernia*
II. *Galanthus lagodechianus* and *G. krasnowii*

1—Epidermal cells
2—Palisade cells
3—Large cavities (*Galanthus lagodechianus*)
4—Very narrow cavities
5—Vascular bundles

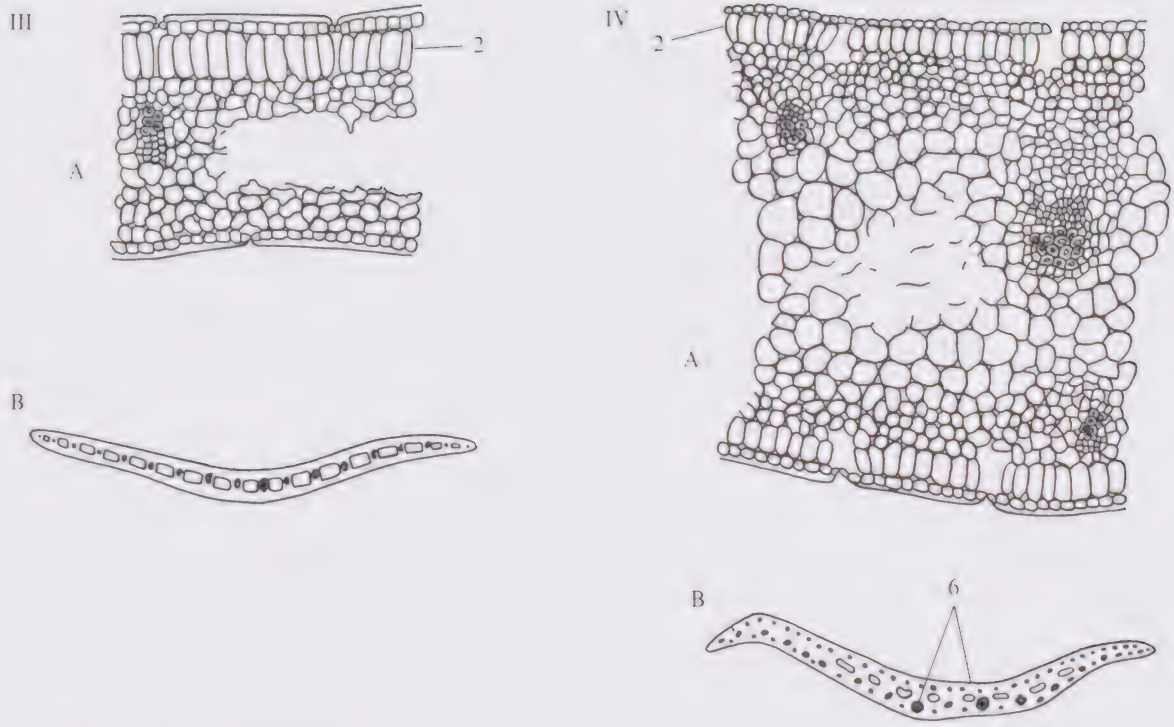


Figure 2. Anatomical structure of the leaves in cross section.

A—Indicates a part of the leaf
B—Indicates the whole leaf

III. *Sternbergia*
IV. *Narcissus*

2—Palisade Cells
6—Two ranges of bundles and small cavities

the ends (Section *Viridifolia*). In different species epidermal cells differ in size, degree of constriction and shape.

Other features of leaf anatomy are also of great importance. One of them is the presence of well developed palisade tissue. In *Ungernia*, *Pancratium* and *Narcissus* palisade cells are arranged in one row and situated under the upper and lower surfaces of the leaf. In *Sternbergia* they occur only under the upper surface of the leaf. In *Galanthus* and *Leucojum* palisade tissue is not developed at all.

Another feature to consider is the presence or absence of cavities between the vascular bundles. These cavities may be large, very narrow and slit-like or be completely absent (Figure 2). The cavities result from breakdown of large, colorless parenchyma cells filled with mucilage, which flows down to the scale when the leaf blade dies.

My research on amaryllid was concerned with the plants growing in the temperate climate (Artyushenko 1970). In the course of my work I came to the conviction that it is necessary to do the same study with representatives of amaryllids from tropical and subtropical regions. But the problem is the absence of the living plants from those in climatic zones.

I ask everyone who is interested in these types of research to contact with me and work together to get new data on Amaryllidaceae.

LITERATURE CITED

Artyushenko, Z. T. 1970. Amaryllisovie (Amaryllidaceae Jaume St. Hilair) USSR. Leningrad.

_____. 1980. Some studies on the vegetative anatomy of *Galanthus* and *Zephyranthes* Amaryllidaceae) and their taxonomic significance. Petaloid Monocotyledons (eds.: Brickell, D. D., C. V. Cutler, and Mary Gregory) Academic Press: London.

Artyushenko, Z. T. and A. V. Schepac 1982. Shoot branching in the representatives of the family Amaryllidaceae. **Botan Journal**, 67(8) :1074-1081.

Dahlgren, R. M., H. T. Clifford and P. F. Yeo. 1985. The families of Monocotyledons. Berlin.

Fedorov, A., M. E. Kirpicznikov and Z. T. Artyushenko 1962. Atlas po opisatelnoi morfologii vishcich rastenji. Stebei i koren. Academy of Sciences, USSR. Leningrad.

Tahtajan, Armen. 1987. Systema Magnoliefitov. Academy of Science. USSR. Leningrad.

Traub, H. P. 1963. The Genera of Amaryllidaceae. American Plant Life Society, 65 pp.

_____, 1967. *Hymenocallis azteciana* Sp. Nov. **Plant Life** 23: 52-54.

SYSTEMATICS AND EVOLUTION OF THE STENOMESSEAE (AMARYLLIDACEAE)

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ABSTRACT

THE central Andes of South America are the major center of diversity for genera of the Amaryllidaceae characterized by $2n = 46$ and usually some measure of staminal connation ("infrafamily" Pancratioidinae Traub *pro parte*). Tribe Stenomesseae comprises the most diverse of these genera. Eight genera, three of which are monotypic, constitute the tribe, and greater than 90% of the species diversity within these genera is concentrated in the central Andean region, particularly Peru and Ecuador. Both species and generic level diversification patterns reflect the tumultuous geological history of the Andean region since the Pliocene (10 million years BP). Defining characteristic of this tribe is a flattened, obliquely winged seed with a phytomelanous testa. *Pamianthe* and *Paramongaia* appear to represent the ancestral clade within the tribe. Two monotypes, *Pucara* and *Mathieua*, are rare relict genera possessing a mosaic of character states. *Stenomesson* is the most polymorphic and the largest genus of this group in the Andean region, and may be directly ancestral to a distinct subgroup of three closely related genera, *Eucrosia*, *Phaedranassa* and *Rauhia*, all with petiolate leaves, a distally channeled scape, and reduction trends in staminal connation. Patterns of character state distribution and phytogeography within and among these genera suggests a scenario of recent mosaic evolution within a tetraploid complex.

INTRODUCTION

The central Andes of South America are the major center of diversity for genera of Amaryllidaceae "infrafamily" Pancratioidinae (Traub 1963), characterized by staminal connation and $2n = 46$. These genera are rare in distribution, and a number of the species are threatened with extinction. Preliminary research suggests that these genera have evolved in the recent geological past (Meerow 1985, 1987a, 1989). The relationships within and among these genera have never been adequately resolved, and their taxonomy has suffered a confusing history.

The Pancratioidinae consists of four tribes (*sensu* Traub 1963): Eucharideae (Pax) Hutchinson (= Euchareae Traub), Eustephieae (Pax) Traub, Pancratieae Salisb. and Stenomesseae Traub. The Eustephieae, consisting of three genera, *Chlidanthus* Herbert, *Eustephia* Cav., and *Hieronymiella* Pax are the most poorly known of the pancratioid genera (see Hunziker 1969).

Traub (1963) considered staminal connation an important delimiting character of the Pancratioidinae. Nonetheless, the presence of a staminal cup by itself does not constitute a basis for aligning tribes, as staminal connation occurs within widely unrelated genera within both "infrafamilies" (Einsiedel 1987; Müller-Doblies 1976).

THE PANCRATIOID BASE

A large, white, fragrant, crateriform flower with a conspicuous staminal cup ("pancratioid," cf. *Pancratium* L.), adapted for sphingid moth pollination (Bauml 1979; Grant 1983; Morton 1965), characterizes at least one genus in each tribe of Traub's (1963) Pancratioidinae. I have used the term "the pancratioid base" to define the five genera of Pancratioidinae with this type of flower morphology (Meerow 1985). These five genera are *Eucharis* Planch. & Lind., *Hymenocallis* Salisb. *sensu str.*, *Pancratium*, *Pamianthe* Stapf, and *Paramongaia* Velarde. All but *Pancratium* are entirely neotropical in distribution. There are only 4 recognized, Paleotropical pancratioid genera, *Pancratium* (ca. 17 species) *Vagaria* Herbert, (ca. 2 species), *Eurycles* Salisb. (2 species), and *Calostemma* Brown (2 species).

Given the apparent degree of homoplasy within and among the tribal lineages of the Pancratioidinae (Meerow 1985, 1987a & b, 1989), a reasonable question is whether the pancratioid base is truely monophyletic. At present, pollen morphology provides the best evidence for a monophyletic Pancratioidinae. The pancratioid flower correlates repeatedly with the largest pollen grain size within the subfamily (Meerow 1985a; Meerow & Dehgan 1985a). The pollen exine of basal pancratioid genera is characteristically coarsely reticulate, and often features a conspicuous dimorphism at the meridional ends. This dimorphism is most extreme in the auriculate pollen grains of *Hymenocallis* (Meerow & Dehgan 1985a, 1988). Nonetheless, independent origin of the pancratioid flower in the paleo-and neotropics respectively cannot be ruled out at this time.

That the neotropical tribes of the Pancratioidinae do represent a monophyletic group is a much more robust hypothesis. Neotropical taxa characteristically have 46 chromosomes (Di Fulvio 1973; Flory 1977; Meerow 1984a, 1985, 1987a, c). A chromosome number of $2n = 22$ is likely ancestral among extant pancratioid genera (Meerow 1984a). This number occurs among widely unrelated genera of Amaryllidaceae (Flory 1977). Base number in the Amaryllidaceae is considered by most workers to be $x = 11$ (Flory 1977; Goldblatt 1976; Meerow 1984a). *Pancratium* and *Vagaria* have 22 chromosomes (Ponnamma 1978); *Eurycles* and *Calostemma* have 20 (Zaman & Chakraborty 1974). The chromosome number $2n = 46$ may have been derived via duplication or fragmentation of a chromosome, followed by doubling of the genome (Lakshmi 1978; Sato 1938).

In three neotropical lineages of the Pancratioidinae, parallel trends in the evolution of floral morphology have occurred (Meerow 1985, 1987a, 1989). In each case, taxa with smaller, tubular or ventricose, brightly colored flowers with reduced staminal connation, and without noticeable fragrance have diverged from taxa possessing the pancratioid flower type. Presumed basal complexes within each pancratioid lineage also have numerous ovules per locule, a character state considered primitive in the Amaryllidaceae (Traub 1963). Each lineage appears to be a monophyletic group on the basis of vegetative and ovarian morphology, as well as chromosome number (Meerow 1985, 1986, 1987a; Traub 1963). A similar pattern occurs in all three lineages: 1) floral morphology of "derived" taxa suggests an ornithophilous pollination syndrome and 2) "derived" taxa are found, entirely or in part, at higher elevations than presumed ancestral taxa. The much higher level of divergence in neotropical pancratioid lineages compared to paleotropical tribes may be primarily a factor of two causes, 1) the uplift of the Andes during the Pliocene (Hammen 1974, 1979), creating much opportunity for geographic isolation, and 2) greater genetic adaptability, via tetraploidy, to new ecological zones (Meerow 1985, 1987a, 1989).

THE STENOMESSEAE

The tribe Stenomesseae is the most diverse of the neotropical pancratioid tribes. Eight genera, three of which are monotypic, constitute the tribe, and greater than 90% of the species diversity within these genera is concentrated in the central Andean region, particularly Peru and Ecuador. Defining characteristics of this tribe are a flattened, obliquely winged seed with a phytomelanous (Huber 1969) testa, and $2n = 46$ (Meerow 1987a; Williams 1981). The tribe contains two small genera, *Pamianthe* (2 species) and *Paramongaia* (monotypic), with pancratioid floral morphology, and a large, polymorphic genus, *Stenomesson* Herbert, with putatively ornithophilous floral morphology. Additional divergence in this lineage is represented by the genera *Eucrosia* Ker-Gawler (7 species), *Phaedranassa* Herbert (9 species), and *Rauhia* Traub (3 species), all of which have petiolate leaves and reduced staminal cups (Meerow 1987a). *Pucara* (Figure 1) Ravenna (1972), a poorly known monotypic genus, possesses an amalgam of morphological characters that suggest a degree of intermediacy between *Pamianthe* and *Paramongaia* on one hand, and also between these latter genera and *Stenomesson*. *Mathieua* Klotzsch, also monotypic, is known only from its fragmentary type (Warcewicz *s. n.*, B). It has been previously allied with *Eucharis* Planch. & Lind. and *Urceolina* Reichb. (Traub 1963, 1971), and recently was placed in the Stenomesseae by Meerow (1987b), largely on the basis of Klotzsch's description of ovary and ovule morphology.

Figure 1. *Pucara leucantha* Ravenna. Photo by Abundio Sagástegui.

PAMIANTHE AND *PARAMONGAIA*.

The two pancratioid genera, *Pamianthe* (Figure 2) and *Paramongaia* (Figure 3) differ chiefly by their respective ecological specializations. *Paramongaia* is adapted to near xeric conditions of the coastal lomas of Peru and western slope vegetation of both Peru and Bolivia (Seibert 1967; Ravenna 1982). *Pamianthe peruviana* is a documented canopy epiphyte in Bolivia (Traub 1967), described therein as *P. cardenasii* Traub), while there is at least circumstantial evidence that *P. parviflora* Meerow is also epiphytic (Meerow 1984b). *Pamianthe* species are white-flowered; *Paramongaia weberbaueri* is yellow-flowered. The free portion of the staminal filament is inserted at the rim of the parandroecium in *Pamianthe*, and below the cup in *Paramongaia*. However, *Stenomesson* is polymorphic for this character, while in *Pucara*, half the filaments are inserted at the cup rim, the remaining three below the rim. Both Williams (1981) and Meerow (1984b) have suggested that separation of *Pamianthe* and *Paramongaia* may ultimately not be justified.

Figure 2. *Pamianthe peruviana* Stapf. Photos by Alan Meerow unless otherwise noted.

STENOMESSON.

Stenomesson Herbert is a moderately-large (35-50 species), polymorphic genus of Amaryllidaceae endemic to the central Andean region (Figures 4-5). It is the largest Andean genus of the Pancratioidinae. With the exception of 3-4 species, the genus is entirely Peruvian in distribution, found primarily above 2000m in elevation. Several species also occur on the coastal loma formations of Peru. Most species are rare in nature, and many are known only from their original descriptions without explicit locality information. *Stenomesson* appears to occupy a position of central importance among genera of Andean Pancratioidinae (Meerow 1985, 1987a). The genus has particular ethnobotanical interest because motifs clearly recognizable as species of *Stenomesson* appear on Incan ceremonial vessels called keros (Vargas 1981). The perianth tube of *Stenomesson* flowers is much longer than the limb, and the perianth is either funnelform-tubular or ventricose in shape. The tube is abruptly constricted near the midpoint of its length. A well-developed staminal cup is usually present. The scape is solid for its entire length.

Figure 3. *Paramongaia* weberbaueri Velarde.

Figure 4. *Stenomesson variegatum* (Ruiz & Pavon) Machr. Photo by Ken Mann.

The first records of the genus were by Ruiz and Pavon (1805), who described *S. coccineum* (Ruiz & Pavon) Herbert, *S. flavum* (Ruiz & Pavon) Herbert, *S. recurvatum* (Ruiz & Pavon)Baker, *S. variegatum* (Ruiz & Pavon) Macbride, and *S. viridiflorum* (Ruiz & Pavon)Benth. & Hook. as species of *Pancratium*. *Stenomesson* was established by Herbert (1821), based on *S. flavum*. Numerous segregate genera were recognized by Herbert (1821) or others (e.g., Ker-Gawler 1824). Traub (1963) recognized three of these taxa as subgenera in *Stenomesson: Callithauma* (Herbert)Traub, *Carpodetes* (Herbert) Traub and *Clinanthus* (Herbert)Traub. Ravenna (1974) has established two others: *Clitanthes* (Herbert)Ravenna and *Fugituba* Ravenna. Neither author has critically assessed the important character states of these subgenera, and their delimitation remains vague. For example, subg. *Callithauma* is distinguished from subg. *Fugituba* only by the insertion of the free filament below the rim of the staminal cup (Traub 1963). Meerow et al. (1986) reported the occurrence of pollen tetrads in one species assigned to subg. *Callithauma* [*S. elwseii* (Baker)Macbr.], the first occurrence of tetrads in Amaryllidaceae *sensu str.* Most recently, Ravenna (1988) reinstated *Callithauma* at the generic rank [monotypic; comprising *C. viridiflorum* (Ruiz & Pavon)Herbert], and also described a new segregate genus, *Anax* Ravenna with two species, *A. mirabilis* (Ravenna)Ravenna, and *A. elwesii* (Baker)Ravenna. Oddly, this places *Stenomesson viridiflorum* and *S. mirabile* in separate genera (*Callithauma* and *Anax* respectively) despite the fact that in floral morphology they are indistinguishable except by perianth coloration.

On the basis of foliar morphology, two main divisions are evident within *Stenomesson*. These divisions cut across most previously demarcated subgeneric lines. One group possesses sessile, linear-lorate leaves that are flat in vernation, and lack a prominent adaxial midrib. The other has petiolate leaves with lanceolate to elliptic laminae which are revolute in vernation and possess a conspicuous adaxial midrib. I have suggested that this latter group may be ancestral to *Eucrosia*, *Phaedranassa* and *Rauhia* (Meerow 1987a). This would make *Stenomesson* at least paraphyletic (*sensu* Hennig 1966). On the basis of character state data, particularly the androecial characters discussed previously, and preliminary cladistic analyses of the Pancratioidinae (Meerow 1984b, 1985), *Stenomesson* may even be polyphyletic.

EUCROSIA, PHAEDRANASSA AND *RAUHIA*.

Eucrosia, *Phaedranassa* and *Rauhia* appear to represent a secondary level of divergence within the Stenomesseae in which the petiolate leaf morphology has become fixed, the scape has a narrow lumen in its distal half, floral tubes are short, and the parandroecium is reduced or obsolete (Meerow 1987a). Ultimately, formal subtribal recognition for this trio may be advisable. The genera are very closely related, and a number of character states are represented mosaically among the three. Intergeneric crosses have been obtained between certain species of *Phaedranassa* and *Eucrosia* and between *Eucrosia* and *Rauhia* (unpubl. data). Distribution of the genera shows a profound correlation with central Andean geological and climatic history since the Pliocene (Berry, 1982; Flenley 1979; Haffer 1974; Hammen 1974; Sillitoe 1974; Simpson 1975, 1979).

Eucrosia (8 species, Figures 6-7) is the most polymorphic of the three genera (Meerow 1987a), and is primarily a xeric, lowland element. The center of distribution and diversity for this genus is western Ecuador. The genus is marked by its zygomorphic flowers with long, declinate, basally connate stamens and androecial nectar glands. Ker-Gawler (1817) established the genus *Eucrosia* with *E. bicolor* Ker-Gawler. The petiolate leaves, irregularly cleft, edentate staminal cup, and the globose nectar glands at the base of the stamens were cited as the primary characters defining the genus. Herbert (1842) erected the genus *Callipsyche* in describing *C. eucrosioides*. While Herbert's choice of epithet acknowledged a similarity

Figure 5. *Stenomesson microstephium* Ravenna. Photo by Timothy Plowman.

Figure 6. *Eucrosia aurantiaca* (Baker) Pax. Photo by Bart Schutzman.

Figure 7. *Eucrosia stricklandii* (Baker) Meerow.

Figure 8. *Phaedranassa schizantha* Baker

Figure 9. *Phaedranassa tunguraguae* Ravenna.

to *Eucrosia*, the reduction of the staminal cup in *C. eucrosioides* was cited as justification for recognizing *Callipsyche* as a distinct genus. Baker (1869a, b) described two additional species of *Callipsyche*, *C. mirabilis* Baker and *C. aurantiaca* Baker. Pax (1888) reduced *Callipsyche* to one of 2 sections of *Eucrosia*. In the last major change concerning the limits of the genus, Meerow and Dehgan (1985b) transferred the monotypic genus *Stricklandia* to *Eucrosia*.

Phaedranassa (9 species, Figures 8-9) is also predominantly Ecuadorean, at middle and upper montane elevations, but 1 species (*P. carmioli* Baker) was described from Costa Rica. The genus is characterized by pink and green, actinomorphic, tubular flowers and completely free stamens. Most of the species are known only from the type localities and from large but local populations in disturbed areas (e.g., road cuts, landslides). Many of the species differ only cryptically from each other, and the genus as a whole exhibits a classic microspecific pattern of diversity (Meerow 1987d).

Rauhia (2-3 species, Figures 10-11) is known only from seasonally dry, middle elevation forests of the upper Marañon and Utcubamba valleys in Peru. This genus is marked by its large, broadly elliptic, carnose leaves that are tessellate when juvenile and have a papilose epidermis. The flowers of all *Rauhia* species are green, and resemble respectively those of a *Phaedranassa* or a *Eucrosia*. Cladistic analysis supports the sister group relationships of these three genera (Meerow 1987a), but also points to very high levels of homoplasy.

Figure 10. Leaves of *Rauhia multiflora* (Kunth) Ravenna emerging from bulb. Photo by James Bauml.

Figure 11. *Rauhia staminosa* Ravenna

The reasons for the diversity of the tribe Stenomesseae are no doubt complex. It may seem facile to single out particular factors, but the geologically recent uplift of the Andean geosyncline (Hammen 1974, 1979) and subsequent changes in vegetation patterns during the Pleistocene (Prance 1982 a and b; Hammen 1974, 1979) have likely been among the most important. The large degree of homoplasy (Meerow 1985, 1987a, 1989), the reoccurrence of a high somatic chromosome number of $2n = 46$ (Di Fulvio 1973; Flory 1976, 1977; Meerow 1987a and b; Williams 1981), and the richness of relict taxa within the tribe suggests a scenario of rapid mosaic evolution (*sensu* Stebbins, 1984) within a monophyletic, tetraploid group.

LITERATURE CITED

Baker, J. G. 1869a. *Callipsyche aurantiaca*. **Refug. Bot.** 3:167.

_____. 1869b. *Callipsyche mirabilis*. **Refug. Bot.** 3:168.

_____. 1888. Handbook of the Amaryllideae. George Bell & Sons, London.

Bauml, J. A. 1979. A study of the genus *Hymenocallis* (Amaryllidaceae) in Mexico. M.S. thesis, Cornell University, Ithaca NY.

Berry , P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). **Ann. Mo. Bot. Gard.** 69:1-198.

Di Fulvio, T. E. 1973. Contribucion al conocimiento cariologico de Amaryllidaceae. Estudio cromosomico en *Hieronymiella* y otras generos afines. **Kurtziana** 7:117-131.

Einsiedel, B. 1987. Morphological studies in the variation of the corona in Amaryllidaceae. Proc. 14th Inter. Bot. Cong., Berlin: 331.

Flenley, J. R. 1979. The Equatorial Rain Forest: A Geological History. Butterworths, London.

Flory, W. S. 1976. Distribution, chromosome number and types of various species and taxa of *Hymenocallis*. **Nucleus** 19:204-227.

_____. 1977. Overview of chromosomal evolution in the Amaryllidaceae. **Nucleus** 20:70-88.

Goldblatt, P. 1976. Chromosome cytology of *Hessea*, *Strumaria*, and *Carpolyza* (Amaryllidaceae). **Ann. Mo. Bot. Gard.** 63:314-320.

Grant, V. 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. **Bot. Gaz.** 144:439-449.

Haffer, J. 1974. Avian speciation in tropical South America. With a systematic study of the Toucans (Ramphastidae) and Jacmars (Galbulidae). Publications of the Nuttall Ornithological Club, No. 14.

Hammen, T. van der 1974. Pleistocene changes of vegetation and climate in tropical South America. **J. Biog.** 1:3-26.

_____. 1979. History of the flora, vegetation and climate in the Colombian Cordillera Oriental during the last five million years. Pp. 25-32 *in* H. Larsen & L. B. Holm-Nielsen (eds.). Tropical Botany. Academic Press, London.

Hennig, W. 1966. Phylogenetic Sytematics. Univ. of Illinois Press, Urbana.

Herbert, W. 1821. *Stenomesson*, *Clinanthes* and *Carpodetes*. **App. Bot. Reg.** 40-41.

_____. 1837. Amaryllidaceae. James Ridgway and Sons, London.

_____. 1842. *Callipsyche eucrosioides*. **Edwards' Bot. Reg.** 28, misc. 49:49-50.

Huber, H. 1969. Die Sammenmerkmale und verwandtschafts verhaltnisse der Liliiflorae. **Mitteil. Bot. Staatssamml. Munchen** 8:219-298.

Hunziker, A. T. 1969. Estudios sobre Amaryllidaceae. III. Sinopsis provisional de *Hieronymiella*, y novedades Argentinas sobre *Zephyranthes*. **Kurtziana** 5:343-367.

Ker-Gawler, J. 1817. *Eucrosia bicolor*. **Edwards' Bot. Reg.** 3: t. 207.

_____. 1824. *Chrysiphiala flava*. **Edwards' Bot. Reg.** 41, pl. 773.

Lakshmi, N. 1978. Cytological studies in two allopolyploid species of the genus *Hymenocallis*. **Cytologia** 43:555-563.

Meerow, A. W. 1984a. Karyotype evolution in the Amaryllidaceae. **Herbertia** 40:139-154.

_____ 1984b. Two new species of pancratioid Amaryllidaceae from Peru and Ecuador. **Brittonia** 36:18-25.

_____ 1985. The evolutionary significance of pancratioid floral morphology in the Amaryllidaceae. **Amer. J. Bot.** 72:962 (Abstract).

_____ 1987a. A monograph of *Eucrosia* (Amaryllidaceae). **Syst. Bot**: 12:460-492.

_____ 1987b. The identities and systematic relationships of *Mathieua* Klotzsch and *Plagiolirion* Baker (Amaryllidaceae). **Taxon** 36:566-572.

_____ 1987c. Chromosome cytology of *Eucharis*, *Caliphruria*, and *Urceolina* (Amaryllidaceae). **Amer. J. Bot.** 74:1559-1575.

_____ 1987d. New species of *Phaedranassa* and *Eucharis* (Amaryllidaceae). **Sida** 12:29-49.

_____ 1989. Systematics of the Amazon lilies, *Eucharis* and *Caliphruria* (Amaryllidaceae). **Ann. Mo. Bot. Gard.** 75:136-217.

_____ and B. Dehgan 1985a. The auriculate pollen grain of *Hymenocallis quitoensis* Herb. (Amaryllidaceae) and its systematic implications. **Amer. J. Bot.** 72:540-547.

_____ 1985b. A new species and a new combination in the genus *Eucrosia* (Amaryllidaceae). **Brittonia** 37:47-55.

_____, N. B. Dehgan and B. Dehgan 1986. Pollen tetrads in *Stenomesson elwseii* (Amaryllidaceae). **Amer. J. Bot.** 73:1642-1644.

Morton, J. K. 1965. The experimental taxonomy of the West African species of *Pancratium* L. (Amaryllidaceae). **Kew Bull.** 19:337-347.

Müller-Doblies, D. 1976. Die zeitliche Korrelation von Laub-und Blutenentfaltung bei den Amaryllioideae. **Ber. Schweiz. Bot. Ges.** 85: 177-178.

Pax, F. 1888. Amaryllidaceae. In: Engler & Prantl (eds.), Die Naturlichen Pflanzen-familien 2: 97-124. Englemann, Leipzig.

Ponnamma, M. G. 1978. Studies on bulbous ornamentals I. Karyomorphology of diploid and triploid taxa of *Pancratium triflorum* Roxb. **Cytologia** 43:717-725.

Prance, G. T. (ed.) 1982a. Biological Diversity in the Tropics. Columbia Univer. Press, New York.

_____ 1982b. A review of the phytogeographic evidences for Pleistocene climate changes in the Neotropics. **Ann. Mo. Bot. Gard.** 69:594-624.

Ravenna, P. F. 1972. *Pucara*, género nuevo de Amaryllidaceae del norte de Perú. **Ann. Mus. Nat. Valparaiso** 5:85-89.

_____ 1974. Contributions to South American Amaryllidaceae VI. **Pl. Life** 30:64-70.

_____ 1982. Contributions to South American Amaryllidaceae IX. **Pl. Life** 38:42-54.

_____ 1988. *Anax* and *Callithauma*, two genera of Amaryllidaceae—Eustephieae from Peru. **Phytologia** 64:215-218.

Ruiz, H. and J. Pavon. 1805 Flora Peruviana et Chilensis 3:54-55

Sato, D. 1938. Karyotype evolution and phylogeny. IV. Karyotype in Amaryllidaceae with special reference to SAT chromosomes. Cytologia 9:203-242.

Seibert, R. J. 1967. "Cojomaria"—*Paramongaia weberbaueri* Velarde, from Peru. **Pl. Life** 23:43-45.

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. **Paleobiology** 1:273-294.

_____ 1979. Quaternary biogeography of the high montane regions of South America. Pp. 157-189, *in* W. E. Duellman (ed.), The South American Herptofauna: Its Origin, Evolution an Dispersal. Monogr. Museum of Natural History, Univ. of Kansas, no. 7.

Sillitoe, R. H. 1974. Tectonic segmentation of the Andes: implications for magmatiosm and metallogeny. **Nature** 250:542-545.

Stebbins, G. L. 1984. Mosaic evolution, mosaic selection and angiosperm phylogeny. **Bot. Jour. Linn. Soc.** 88:149-164.

Traub, H. P. 1963. Genera of the Amaryllidaceae. American Plant Life Society, La Jolla.

_____ 1967. *Pamianthe cardenasii*, sp. nov. **Pl. Life** 28:46-48.

_____ 1971. Amaryllid Notes. **Pl. Life** 27:57-59.

Vargas, F. C. 1981. Plant motifs on Inca ceremonial vases from Peru. **Bot. J. Linn. Soc.** 82:313-325.

Williams, M. D. 1981. Chromosome count for *Paramongaia weberbaueri* Velarde. **Pl. Life** 37:83-89.

Zaman, M. A. and B. N. Chakraborty. 1974. Cytogenetics of Amaryllidaceae: I. Karyomorphology and meiotic behavior of inversion heterozygote *Eurycles sylvestris* Salisb. **Bangladesh J. Bot.** 3:51-58.

MORPHOLOGICAL VARIATION IN A POPULATION OF *HIPPEASTRUM* HERB.

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WORKING in the systematics of *Hippeastrum*, attention is called to the fact that most, or nearly all, species descriptions are based on very few specimens, sometimes just on one. They are generally written by someone who has not visited any natural populations and probably has never analyzed a large one. *Hippeastrum* populations commonly appear as small, scattered clusters or groups resembling very small populations, but sometimes a thorough scanning of a large area will show more groups, collectively forming a larger population. However, the populations can sometimes be small and so scattered, and since the pollinating agent, or its range of activity, is not known, it becomes difficult to establish where and when genetic material is exchanged. It is rare to find really large populations with thousands of individuals in close proximity where phenological and cytological variability can be observed. Consequently, many species were described, based on small differences in external features.

Several monocotyledons, when dried for herbarium specimens, can lose many of their distinguishing characteristics, such as colors, form and position of the flowers. Therefore, much of the variation has to be studied in natural populations, where all the features can be observed without the interference of a change in the environment. Perhaps as a consequence there are not many taxonomists who work in these groups, and the taxonomy at the species and generic levels, sometimes even at the family level, can be rather confused and without clear boundaries. What adds to this confusion is the ability to reproduce vegetatively which can turn one clone, i.e. genetically one individual, into what seems like a whole population, maintain very old clones, and establish new clones with low fertility because of aneuploidy or interspecific crossings. These "unadapted for crossing" clones, if well adapted for survival and vegetative reproduction, can produce a constant "noise" in the reproductive history of the group that makes it more difficult to establish clear didactic characteristics and boundaries for the species. This can lead to two kinds of extremes: (1) the overrating of some features, so small differences lead to descriptions of new species, rather than the extremes of variation of a single species, or, (2) the overlooking some features, resulting in several species being treated as one. Additionally, many of the newer descriptions of *Hippeastrum* do not discuss the older ones with similar descriptions.

This paper will introduce some observations of a very large population found near the town of Atibaia, state of São Paulo, Brasil. In this locality our group found three obviously different species growing close together.

One group in the woods in the lower part of the hill, was identified as *Hippeastrum striatum* (Lam.)Moore. Scattered clones were encountered. These produce many bulbils and flower lavishly. People who live in these areas like to plant them near their houses, but in more or less wild environments.

In the same woods, but growing on the rocks, another species is found, identified as the true *Hippeastrum psittacinum* (Ker-Gawl.)Herb. as illustrated by Ker-Gawler (1817) in the original description of the species. This species is also found on the higher part of the hill, on rocks, but always more or less in shade, forming a large population with thousands of individuals.

In the open, more exposed and sunny places of rocks, on the sides and top of the hill there is another species, denominated *Amaryllis* sp. (*sensu* Traub) "atibaya" (sic) by Blossfeld (1979). (The taxon was not validly described, and the author put the name between inverted commas, but the name has been used in later works.) This species also forms a very large population with thousands of individuals.

Both species *Hippeastrum psittacinum* and *Hippeastrum* sp. "atibaya" form clones with bulbs that stay together, forming clusters, or groups, with big bulbs. *Hippeastrum* especially forms very big bulbs, the oldest ones more than 10cm in diameter and with long necks (± 15cm). It is thus very easy to tell both species apart even without flowers. They may, however, grow side-by-side and sometimes apparent hybrids can be found. Both species have $2n=22$ chromosomes and in the greenhouse hybridize easily in both directions. The *Hippeastrum* population was more extensively analyzed and showed some individuals with $2n=23$ and some with $2n=24$ chromosomes. It was probably one of those individuals that was analyzed by Flory and Coulthard (1981) who found $2n=24$ chromosomes. It was even possible to obtain a meiosis figure with 23 chromosomes and a pollen grain mitosis with 12 chromosomes, (Figures 1 and 2; and Dutilh 1987).

Figure 1. Meiosis in *Hippeastrum* sp. "atibaya" with 11 bivalents and 1 univalent. (×1.600) All photographs by Julie Dutilh.

Figure 2. Mitosis in a pollen grain with 12 chromosomes. (×900)

The fact that microsporogenesis showed 11 bivalents and one monovalent could mean that the extra chromosome had no homology with the chromosomes of the normal A complement, but is a B chromosome (Jones 1975). Alternatively, there may be a strict genetic control of the meiosis process which does not permit the pairing of more than two chromosomes, even if the plant is an aneuploid and there is homology between the extra chromosome and the chromosomes of the normal complement.

The morphological variability found in *Hippeastrum* is more or less illustrated in the photographs. In general, the features that vary are: flower color (from brighter, darker orange red to rosier and salmon colored flowers with a more or less evident reticulation); flower size (tepals from 9 to 15cm long and 2.5 to 4.5cm wide, giving proportions of 2:4; up to 5:1) form of the tepals (from nearly triangular to much narrower at the base, with many intermediate forms); length of the whitish, yellowish and greenish stripe that can extend from about ⅛ to ¾ of the length of the tepals; differences in the bearing of the flowers (more or less open, more or less upstanding, laterally or dorsiventrally compressed). Additionally, the tepals can be more or less undulated. Generally, there are two but there can be three flowers. The spathe generally withers when the flower opens, but can stay green and upright until after the flower withers, (Figures 3 to 6).

It had not previously been possible to correlate the external morphological variation to the cytological variation, but now access has been given to a more protected area. A plan is being made to study the reproductive biology of the population in detail.

It is hoped that this study will elucidate some of the population dynamics of the area and give an idea about the reproductive biology of the species of this genus. This knowledge can help establish more natural species characteristics and boundaries that satisfies our need for an organized taxonomic system in further studies and also reflect, with some fidelity, its biological dynamics.

LITERATURE CITED

Blossfeld, H. 1979. Notes on an *Amaryllis* species from Brasil. **Plant Life** 35:17-19.

Dutilh, J.H.A. 1987. Investigacões citotaxonômicas em populacões brasileiras de *Hippeastrum* Herb. Master's Thesis, Universidade Estadual de Campinas, Brasil.

Flory, W.S. and R.F. Coulthard 1981. New chromosome counts, numbers and types in genus *Amaryllis*. **Plant Life** 37:43-56.

Ker-Gawler, J.B. 1817. *Amaryllis psittacina*. **Bot. Reg.** 3:99.

Jones, R.N. 1975. B Chromosome system in flowering plants and animal species. **Int. Rev. Cytol.** 40:1-100.

Figure 3–6. *Hippeastrum* sp. "atibaya". All photographs were taken at the same population, note the differences in shape, color, and orientation of the tepals and flower. Scale 5cm long with a 1cm² reticulation.

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CHROMOSOMAL EVOLUTION IN THE GENUS *LYCORIS*

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ABSTRACT

BASED on chromosomal morphology and nuclear DNA content in 12 strains belonging to 8 species and 1 hybrid clone of the genus *Lycoris*, the authors considered chromosomal evolution of this genus. Karyotypes of *Lycoris* species are constituted of 22 chromosome arms in diploid species and 33 arms in triploids with an exception in *L. incarnata* which is triploid with a very small, extra fragment of chromosome. However, they are different among species or even among different plants in a single species in number of V-shaped chromosomes resulted from Robertsonian translocation of two rod chromosomes and are characterized by continuous variation in chromosome length. 2C DNA content of individual nucleus in single layered epidermal cell of the basal part of the well developed leaf was measured Fulgen-cytophotometrically. There is a close proportionality ($r = 0.92$) between total chromosome length and relative DNA content of the nucleus. This fact indicates that the small segment seems to have occurred at the time of formation of the V-shaped chromosomes from rod-shaped ones during evolution in this genus.

INTRODUCTION

The genus *Lycoris* is divided into two subgenera. Species belonging to subgenus *Symmanthus* develop or emerge leaves in early spring. Another subgenus, *Lycoris* emerges leaves in autumn. *Lycoris* species are characterized by two kinds of chromosome, short telo-or acro-(rod) and long metacentric (V-shaped) chromosomes which apparently are distinguishable from one another. Inariyama (1951a, b) considered that V-shaped ones had been formed by fusion at centrometric region of two rod chromosomes or Robertsonian change. Alternative hypothesis that two rods resulted from the fission of one V-shaped chromosome at centrometric region, was also proposed (Kurita 1988).

Nishikawa *et al*. (1979) confirmed in six strains belonging to five species of *Lycoris* that any V-shaped chromosome was by far longer than the sum of two rods and clearly demonstrated that the more V-shaped chromosome a species had, the longer total chromosome length and the more nuclear DNA content. This suggests that the evolution of chromosomes in *Lycoris* is not simple fusion or fission, but accompanied with gain or loss of chromatin.

In order to expand this finding based on only six strains of *Lycoris* in the previous study to the whole genus, cytophotometrical DNA determination and karyotypical analysis of 12 strains of 8 species and one F_1, hybrid clone, including previously studied strains, was carried out in this study.

MATERIALS AND METHODS

Twelve strains of 8 species and one hybrid clone or cultivar "Jacksonian" were used in the present study (Table 1). Two clones (A and B) of *L. albiflora* were introduced from different sources and somewhat different from one another in flowering morphology. For karyotype analysis, root tips were pretreated in 0 °C ice water for 24 hours and fixed in fresh Farmer's fluid. Root tips stained in aceto-carmine were squashed. Chromosome length was measured from 15 to 53 metaphase plates microphotographed.

Nishikawa *et al*. (1979) measured DNA content of the single-layer epidermal cells of the inner side of the scale of the bulb, but the authors used the epidermal 2C cells of the basal part of well developed leaf in the present study since peeling off the epidermal cells of the bulb disrupts propagation.

The single-layer epidermal tissues were peeled off from the basal part of leaf, fixed in fresh Farmer's fluid for one week, rinsed in ethanol series and stocked in 75% ethanol in a refrigerator. Five samples of 4 strains and hybrid clone, "Jacksonian" (*L. sprengeri*×*pumila*) as the standard, were simultaneously hydrolysed in 1N HCl at 60 °C for ten minutes, stained in Schiff's reagent for 3 hours, washed in pirosulfite solution twice for 15 minutes each, dehydrate, permanently sealed side by side on one glass and measured in short period of time. Nikon-Vickers M85 Scanning Microdensitometer was used for the measurement of nuclear DNA content.

RESULTS AND DISCUSSION

The chromosome complement of 13 clones analyzed in the present study is ideogramed in Figure 1. Numerical data of chromosomes are summarized in Table 1. All strains, except for *L. incarnata*, have very small chromosome fragment in addition to 25 rod and 4 V-shaped chromosomes, suggesting that formation of one small and one V-shaped chromosomes by reciprocal translocation occurred near the centrometric region of two rod chromosomes in this strain. At a glance of Figure 1, it is apparent that rod chromosomes in every strain vary continuously in their length. Moreover, the variation of chromosome length is very similar among four diploids and one triploid strains consisting of only rod chromosomes (Figure 1, Table 1). The variation of rod chromosomes in *L. sanguinea* 3x which has one V-shaped chromosome, was also similar to five strains of only rod chromosomes, suggesting recent origin of this triploid strain from diploid of *L. sanguinea*. Kurita (personal communication) found this triploid in a diploid population of *L. sanguinea*. Two or four rods in *L. aurea* were very long. Five strains having more than three V-shaped chromosomes, especially *L. houdyshelli*, two strains of *L. albiflora* showed larger variation in length of rod chromosomes. The shortest V-chromosome in *L. incarnata* was very short in comparison with V-shaped ones found in other species. Morphology of three V's in *L. houdyshelli* was very similar. The B line of *L. albiflora* had cream colored flowers with reddish spots in the central part, fewer of flowers per plant (6-9 in A versus 4-7 in B line), somewhat longer and wider petals, shorter flower stalk and 17% longer bulb diameter than A line. The longest rod chromosomes in two clones of *L. albiflora* A and B are different from one another. The longest rod chromosome in B line was not a telo- nor acrocentric, but a subtelocentric chromosome. No other karyotypic differences were observed between studied clones of *L. albiflora*.

With one exception, the shortest one in *L. incarnata*, even the shortest V-chromosomes in seven strains were much longer than twice the shortest rod chromosomes. The longest V-shape chromosomes in all eight clones have similar lengths or are longer than twice the longest rod in each strain. Variance analysis of total chromosome length revealed signifi-

Table 1. Total chromosome length and nuclear DNA content in 13 strains of *Lycoris*.

Species or strain	*2n*	Karyotype[1)]	Total chromosome length (μm)			Nuclear DNA content[3)]		
			No. of cells	Mean±SE	Ratio[2)]	No. of cells	Mean±SE	Ratio
L. sanguinea	22	22R	23	247± 6	0.93	180	56.4±0.3	1.16
L. sanguinea 3*x*	33	31R+1V	24	464±10	1.75	150	80.8±0.3	1.66
L. sprengeri	22	22R	15	243± 7	0.92	150	52.6±0.2	1.08
L. incarnata	34	25R+4V+1F(B)	15	400± 8	1.51	360	80.4±0.3	1.65
L. squamigera	33	21R+6V	15	408± 9	1.54	240	89.8±0.3	1.85
L. radiata var. *pumila*	22	22R	18	265± 9	1.00	150	48.6±0.4	1.00
L. radiata	33	33R	16	386± 7	1.46	240	71.6±0.3	1.47
L. aurea	22	2R+ 10V	15	363±15	1.37	180	71.0±0.4	1.46
L. aurea	22	4R+9V	18	337± 9	1.27	150	70.9±0.3	1.46
L. houdyshelli	33	27R+3V	15	370± 9	1.40	180	77.1±0.4	1.59
L. albiflora A	22	12R+5V	53	286± 5	1.08	570	60.6±0.3	1.25
L. albilfora B	22	12R+5V	35	291± 7	1.10	330	60.7±0.3	1.25
Jacksoniana	22	22R	21	256± 6	0.97	1260	50.0±0.1	1.03

[1)] R, V and F(B) indicate rod, V-shaped and fragment chromosome, respectively

[2)] arbitrary unit

[3)] ratio to that of *L. radiata* var. *pumila*

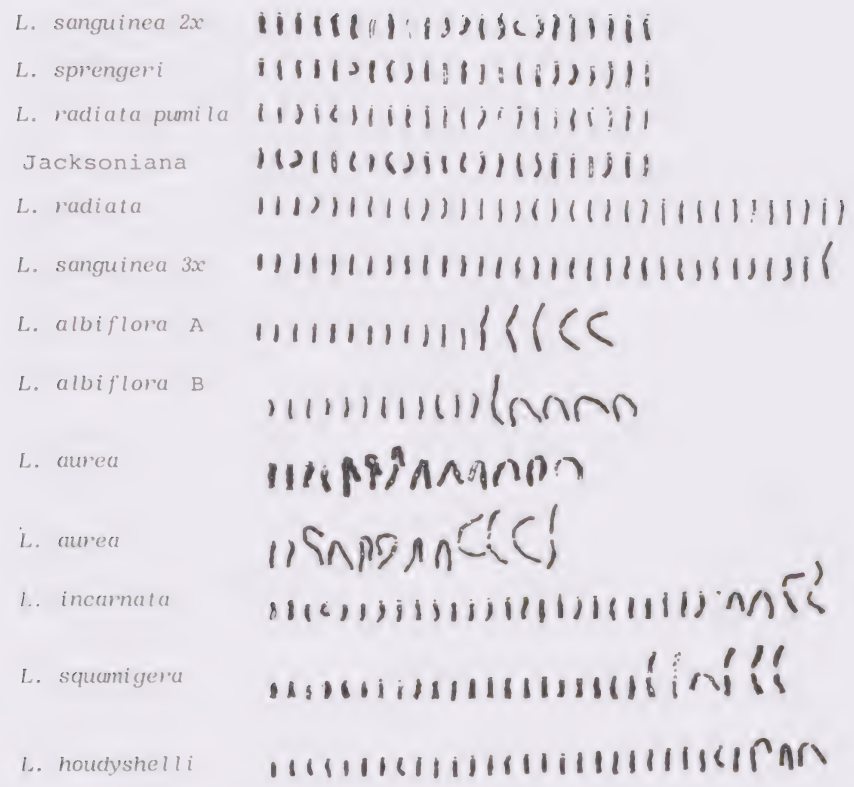

Figure 1. Karyotypes of 13 strains in *Lycoris* analyzed in the present study.

cant difference among strains (Table 1). *L. sanguinea* 3*x* has the longest total chromosome length among strains analyzed here and 1.88 times of diploid of this species. Four strains constituting only rod chromosomes, i.e. *L. sanguinea*, *L. sprengeri*, *L. radiata* var. *pumila* and "Jacksonian," have similar total chromosome lengths (Table 1). No significant difference was observed between two strains of *L. albiflora*. Total chromosome length in triploid *L. radiata* is 1.46 times its diploid relative, *L. radiata pumila* but the former has only two satellite chromosomes, as in the latter. It is also a well known phenomenon in higher plants that the number of satellite chromosomes or secondary constrictions does not increase proportionally with polyploidy. The number of satellite chromosomes in this genus will be reported and considered elsewhere in detail.

Nuclear DNA content at the interphase stage in basal part of leaf and in inner scales of the bulb was the same as that of anaphase in the nucleus in scale cells or was half of that at metaphase of scale cells, indicating uniform 2C DNA class in epidermal cell of leaf and inner scale cell.

Nuclear DNA content is statistically different among 13 strains (Table 1). Of course, no difference was observed in two strains of a single species, *L. albiflora* (A and B) and *L. aurea*

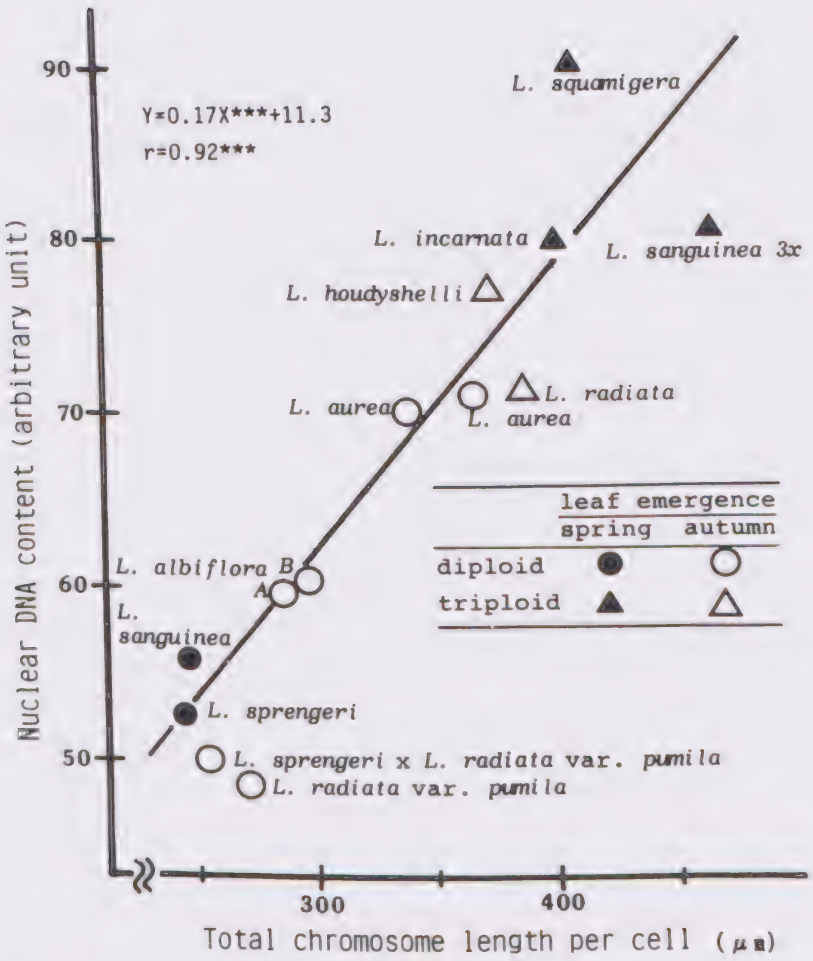

Figure 2. Relationship between nuclear DNA content and total chromosome length.

(2R + 10V and 4R + 9V types), respectively. On the other hand, significant differences were observed among four diploid species or clone constituting only of rod chromosomes, i.e. *L. sanguinea*, *L. sprengeri*, *L. radiata* var. *pumila* and 'Jacksoniana.' The DNA content of 'Jacksonian' is very similar to the expected value from parental DNA content, i.e. *L. sprengeri* and *L. radiata* var. *pumila*. Takemura (1962) demonstrated that *L. albiflora* (5V + 12R) was very derived from *L.* aurea (2R + 10V) and *L. radiata* var. *pumila* (22R) by hybridization. This parentage is also supported by nuclear DNA content. *L. radiata* is an autotriploid of *L. radiata* var. *pumila* and had 1.47 times the DNA of related diploid, the *L. radiata* var. *pumila*. As compared with diploid, the triploid, *L. sanguinea* was 1.88 times longer in total chromosome length, but 1.43 times more in DNA content of the nucleus. This fact suggests loss of small chromosome segment(s) accompanied with formation of V-shaped chromosomes

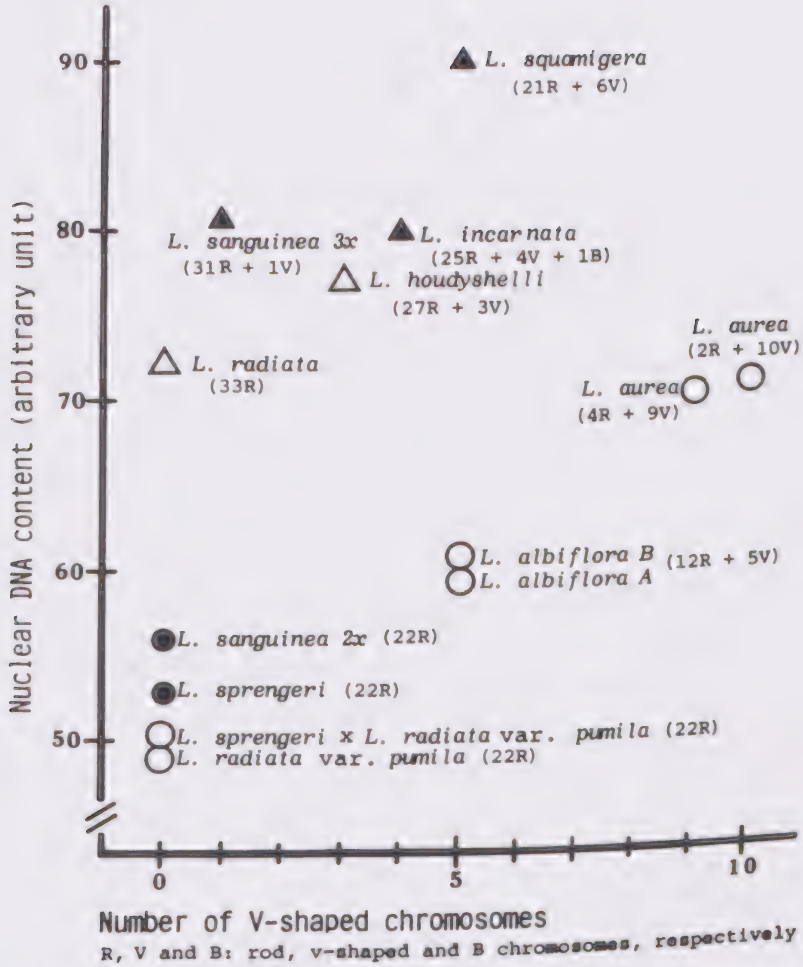

Figure 3. Relationship between nuclear DNA content and total number of V-shaped chromosomes

by Robertsonian translocation in *L. sanguinea* 3x. It is apparent that chromosome length or total chromosome length was sometimes considerably variable owing to conditions of pretreatment, stage of metaphase observed, squashing and so on. Morphology of the leaf and bulb of *L. sanguinea* 3x is very similar to those of diploid *L. sanguinea*. By comparison of the morphology between *L. squamigera* and synthesized triploid hybrids, Takemura (1961) confirmed Inariyama's hypothesis about the origin of *L. squamigera* (10R + 6V, DNA content in this study; 89.8) which is derived from *L. straminea* (10R + 6V) and *L. sprengeri* (22R, 52.6). Unfortunately, one putative parent of *L. straminea* was not available in the present study, the DNA value of *L. straminea* would be expected to be 63.5, however. This expected DNA value of *L. straminea* is similar to the estimated value from the formula based on the

present data and the relationship between nuclear DNA content and number of V-shaped chromosomes (Figure 3).

Based on the basic karyotype theory (Inariyama 1951b), it is likely that *L. houdyshelli* (27R + 3V) is a triploid hybrid between the normal gamete (5R + 3V) of *L. straminea* (10R + 6V) and the unreduced gamete generated in an unknown diploid (22R). Among three diploid species with 22R, *L. radiata* var. *pumila* (DNA value; 48.6) is the most suitable diploid as a donor of reduced gamete (DNA value; 45.4). This parentage is supported by leaf emergence seasonality. *L. houdyshelli* develops leafs out in the fall and belongs to subgenus *Lycoris*. The putative parent, *L. straminea* belongs to another subgenus, *Symmanthus* on the other hand. Then, *L. radiata pumila* is only one diploid species having 22R in this subgenus.

The relationship between nuclear DNA content and total chromosome length per cell or number of V-shaped chromosomes are shown in Figure 2 and Figure 3, respectively. Since significantly high correlation (r=0.92) between nuclear DNA content and total chromosome length is observed, variation in nuclear DNA content of *Lycoris* species is attributed to the length of chromosomes on which chromatin or DNA distributes longitudinally evenly. As shown in Figure 1, all chromosomes were strained uniformly in aceto-carmine. Moreover, Feulgen-stained nuclei of the epidermal cells did not have any distinct heterochromatic body. Preliminary Giemsa banding did not reveal any bands in chromosomes of *L. albiflora*. Nishikawa *et al.* (1979) pointed out in 6 strains of 5 species of *Lycoris* that the more the number of V's, the longer the total chromosome length and the more DNA content of the nucleus. The present study confirms the previous result of analyzing 13 strains of *Lycoris* and reveals a similar trend of increasing nuclear DNA content associated with the number of V-shaped chromosomes in both diploid and triploid species. This fact indicates that the small segment of chromosome on both sides of the centromere is responsible for the increase in DNA content. This increase of DNA in centromeric regions seems to have occurred in the progress of formation and/or cytological stabilization of the V-shaped chromosomes from two rod-shaped ones during the evolution in this plant group. More detailed consideration will be reported elsewhere.

LITERATURE CITED

Inariyama, S. 1951a. Cytological studies in the *Lycoris* (I) **Sci. Rep. Tokyo Bunri Daigaku**, Sect. B. 6: 74-100.

Inariyama, S. 1951b. Cytological studies in the genus *Lycoris* (II). **Sci. Rep. Tokyo Bunri Daigaku**, Sect.B. 7:103-157.

Kurita, S. 1988 Variation and Evolution in the karyotype of *Lycoris*, Amaryllidaceae VII. Modes of karyotype alteration with species and probable trend of karyotype evolution in the genus. **Cytologia** 53: 323-335.

Nishikawa, K.Y. Furta, and H. Endo 1979. Consideration of the chromosome evolution on the basis of nuclear DNA content and total chromosome length in *Lycoris*. **Japan J. Genetics** 54:384-396.

Takemura E. 1961 Morphological and cytological studies of artificial hybrids in genus *Lycoris* I. (On the F, hybrid between L. sprengeri and L. straminea). **Bot. Mag. Tokyo** 74:524-531 (in Japanese).

Takemura, E. 1962. Morphological and cytological studies of artificial hybrids in genus Lycoris III. (Artificial hybrids having 4 V-shaped chromosomes). **Bot. Mag. Tokyo** 75:324-330 (in Japanese).

CYTOGENETICS IN THE GENUS *ALSTROEMERIA*

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INTRODUCTION

CHROMOSOME studies in the genus *Alstroemeria* are among the very earliest ones in plant cytology. The first paper on the chromosomes of *Alstroemeria* was published by Strasburger (1882). However, the total number of chromosome studies in the genus *Alstroemeria* in the last 100 years is surprisingly small with a total of less than 10 or so species studied (Darlington and Wylie, 1955, Hang and Tsuchyia 1988, Tsuchyia *et al.* 1987).

Most of the papers published before 1942 were the results of studies with the old paraffin section method and some details are questionable (Sato 1938, Taylor 1926, Whyte 1929). The results of some recent papers are also questionable with respect to detailed karyotypes (Lakshmi 1976), in spite of recent progress in cytological techniques.

In this article, the results of chromosome studies in various wild species and some cultivars are described with special emphasis on the analysis of karyotype, meiotic chromosome behavior and pollen fertility.

MATERIALS AND METHODS

Plants and seeds of various species were obtained from the Department of Horticulture, Colorado State University, The Denver Botanic Garden & Isamu Miyake of Japan, R. Wygnanki of Chile, and several other workers. Most of the cultivated varieties were obtained from the Department of Horticulture, Colorado State University, the Denver Botanic Gardens, and others.

Somatic chromosomes were studied in root-tip cells with the aceto-carmine squash or lacto-propionic orcein method. Details were previously reported (Tsuchyia *et al.* 1987).

Meiotic chromosomes were studied with aceto-carmine or aceto-orcein squash methods. Pollen fertility was studied with the slides stained with diluted (0.2%) aceto-carmine solution.

RESULTS

1. Chromosome number

The somatic chromosome number of all eleven species were $2n=2x=16$ (Table 1). Figures 1 and 2 are flowers (1a, 2a) and somatic metaphase chromosomes (1b, 2b) of *A. aurantiaca* and *A. psittacina*, respectively.

Twenty-five cultivars were studied with the following results:

$2n=2x=16$	4 cultivars
$2n=3x=24$	12 cultivars
$2n=3x+1=25$	1 cultivar
$2n=4x-1=31$	1 cultivar
$2n=4x=32$	6 cultivars
$2n=4x+1=33$	1 cultivar

Also, *A. ligtu* hybrids showed the diploid chromosome number, $2n=2x=16$.

2. Karyotype analysis

Origin or pedigree of most of the cultivars is not known. A preliminary study of chromosome constitutions in many cultivars and some species showed that it may be possible to determine the putative parental species used in a breeding program, at least in some cases, if detailed information is available on the karyotypes of the wild species involved. Four diploid cultivars showed different karyotypes from any of the species so far studied. Several chromosomes were not morphologically homologous pairs. Several *A. ligtu* hybrids also showed unique karyotypes with two special chromosome pairs with tiny satellites on their short arms.

It is therefore important to study karyotypes first in various species. Information on the plant characteristics such as twisting and hairiness of leaves, types and colors of flowers would also be used together with the results of karyotype analysis.

First attempt was the conventional karyotype analysis. Preliminary karyotype analysis showed variations between species in different degrees; some species had rather similar karyotypes with minor differences. Other species showed considerable differences from others. Also, karyotypic polymorphism was found in the different plants within a species such as *A. versicolor*.

However, most of the species so far studied had a common chromosome constitution consisting of two groups of four chromosomes in their genomes. The first group consists of four pairs of metacentric, submetacentric or subtelocentric chromosomes of different sizes. Most of these chromosomes do not have satellite. The second group contains four pairs of acrocentric chromosomes with a long, long arm and a very short, short arm, of almost same total length with or without satellite, although the total lengths were different in some species.

However, *A. ligtu* and *A. ligtu* hybrids showed deviation from this "general" karyotype in *Alstroemeria*. The first group consisted of five chromosomes including two satellited chromosomes, and the second group had only three chromosomes with or without satellite (Rustanius 1986, Tsuchyia *et al.* 1987).

In order to study more details of the structure of chromosomes, the Giemsa-banding technique was applied to several species and cultivars. This analysis provided some interesting information on the chromosomal structural variations within a complement and between different species. The Giemsa-banding technique also provided considerable detail of the chromosome structure. Even morphologically similar "homologous chromosomes" showed distinct difference in banding patterns in some cases.

Preliminary results also indicated that some species such as *A. psittacina* and *A. pelegrina* showed only a limited number of bands in most of the chromosomes, although more detailed analysis is necessary to reach a final conclusion on this matter. Interestingly, Giemsa banding analysis showed several unbanded chromosomes in some diploid cultivars such as 'Zebra' and 'Eureka', indicating that some of the parental species may have chromosomes which do

not show Giemsa bands. Preliminary results indicated that *A. psittacina* and *A. pelegrina* may not have prominent Giemsa bands (Hang and Tsuchiya, unpublished). It is necessary, however, to study more species to determine the parental species involved in the development of these varieties.

3. Meiosis in *Alstroemeria*

Chromsome configurations in Metaphase I were studied in several species (Table 1) and some cultivars.

Most of the species showed 8 bivalents (8_{II}) in all sporocytes analyzed. However, *A. ligtu*, *A. pelegrina*, and *A. pulchra* showed $7_{II}+2_{I}$ in some sporocytes, although a majority of sporocytes had 8 bivalents. Figures 3 and 4 show meiotic MI configurations of 8_{II} in *A. aurantiaca* and *A. psittacina*, respectively.

Meiotic chromosome behavior of *A. ligtu* hybrids (Figure 5) and Dr. Salter's hybrids was rather normal showing 8 bivalents at meiotic metaphase in most of the sporocytes. However, many cultivars showed highly abnormal meiotic behavior, even some diploid cultivars (Figure 6). At metaphase I of meiosis in triploid cultivars, most of the chromosomes were univalents with a few bivalents, some of which were heteromorphic pairs. Tetraploids often showed many bivalents and a few trivalents and/or univalents at MI.

Table 1. Somatic chromosome numbers (2n), meiotic (MI) configurations and pollen fertilities in 11 species of *Alstroemeria*.

Species	Chromosome No. (2*n*)	Meiotic (MI) configuration	Pollen fertility (%)
A. aurantiaca D. Don	16	8_{II}	—
A. caryophyllaea Jacq.	16	—	—
A. chilensis Cree	16	—	—
A. haemantha Ruiz et Pavon.	16	8_{II}	—
A. hookeri Loddiges	16	—	93
A. ligtu L.	16	8_{II}, 7_{II} + 2_{I}	97
A. pelegrina L. *alba*	16	—	84
A. pelegrina L. *rosea*	16	8_{II}, 7_{II} + 2_{I}	37
A. psittacina Lehm.	16	8_{II}	91
A. pulchella L.*	16	8_{II}	—
A. pulchra Sims	16	8_{II}, 7_{II} + 2_{I}	78
A. versicolor Ruiz et Parvon.	16	8_{II}	98
A. violacea Phil.	16	8_{II}	80

* Synonym of *A. psittacina*

Pollen Fertility

Pollen fertility was studied in many species (Table 1) and cultivars. Generally speaking, most of the species with normal meiotic behavior showed high pollen fertility ranging from 80% to 98% good pollen. However, the pollen fertility in the species with abnormal meiotic behavior varied considerably, ranging from 37% in *A. pelegrina rosea* to 97% in *A. ligtu*.

The pollen fertility in the cultivars also correlated with meiotic behavior, at least to some extent. For example, *ligtu* hybrids showing highly normal meiosis with 8 bivalents at MI had 98% and tetraploid cultivars 'Luciana' ($2n=31$) and 'Jubilee' ($2n=32$) had 75% and 64%, respectively. However, pollen fertilities of diploid and triploid cultivars which showed highly abnormal meiotic behavior had pollen fertility of 4% to 8%. An exception was a cultivar Orange Beauty, a hypertriploid with $2n=25$ ($3x+1$) chromosomes, having 40–50% pollen fertility.

DISCUSSION

It was a surprise to find a high percentage of polyploids among the cultivars studied in view of the fact that all wild species so far studied showed the diploid number of $2n=16$ (Hang and Tsuchiya 1988, Tsuchiya 1986: Table 1). This indicates that the polyploidy method has been used in *Alstroemeria* breeding program, together with the mutation method (Broertjes and Verboom 1974).

The pedigrees of most of the cultivars are not known to the public. One of the objectives in *Alstroemeria* cytology is the determination of probable parental species in cultivar development. It is obvious from brief karyotypic studies in many cultivars that karyotype analysis in various wild species is essential to accomplish the objective. Preliminary results from conventional karyotype analysis and the Giemsa-banding technique have shown that detailed information on the chromosomal constitutions in wild species would be very useful in determination of putative parental species utilized for cultivar development in *Alstroemeria*.

The karyotype studies with the use of conventional and Giemsa-banding techniques will also provide useful information on the evolutionary and phylogenetic relationships among species. Giemsa-banding techniques have already provided important information on the nature of chromosomal polymorphism between presumed homologous chromosomes and between plants within a species.

Meiotic chromosome analysis provided important information on the genetic and cytological stability of various species and on the cause of pollen and/or seed fertility (sterility) in both species and cultivars. Generally, species with normal meiotic behavior had higher pollen fertility and some seed sets. Pollen fertility is an important indicator for seed fertility. The results so far obtained showed fairly good correlation between pollen fertility and seed set by selfing and sib-crossing. It was also found that pollen fertility correlated fairly well with meiotic behavior of chromosome, especially chromosome association at metaphase I in meiosis. The relatively or highly abnormal meiotic behavior of some cultivars was also reflected in high or very high pollen sterility. Analysis of meiotic behavior in some interspecific hybrids may also provide useful information on their phylogenetic relationships in the future work.

Another aspect to be pointed out is the fairly good pollen fertility in tetraploid and near tetraploid cultivars ($2n=31$, 32, and 33) and one hypertriploid ($2n=25$). These cultivars are definitely useful for further cultivar development by crosses with other cultivars or wild species.

The results presented in this article are still preliminary in most of the aspects. Also the materials studied are rather limited: only 11 species among some 70 or more species and 27 cultivars including two hybrids, *A. ligtu* hybrids and Dr. Salter's hybrids among more than 100 cultivars were studied. It is important to study many more species and some more cultivars. Detailed karyotypic studies in many species with both conventional and Giemsa-banding techniques are particularly important in view of cytological interest and practical application.

Figures 1-2. Flowers and somatic metaphase chromosomes in two species. 1a, flowers and 1b, somatic chromosomes in *A. aurantiaca*. 2a, flowers and 2b, somatic chromosomes in *A. psittacina*.

Another important item is cytogenetic studies of interspecific hybrids for understanding the evolutionary relationships in terms of chromosomal variations.

One more objective to be included for future work is the genetic analysis of various characteristics such as leaf traits, flower colors, and spotted/striped character. Without genetic information, breeders have to continue the rather old breeding methods of trial-and-error. If the genetic nature of various characters is analyzed, breeding of *Alstroemeria* may be conducted systematically.

SUMMARY

Chromosome numbers of 11 wild species of *Alstroemeria* were all $2n=2x=16$. Karyotype analysis by conventional and Giemsa-banding techniques showed intraspecific and interspecific variations. Meiosis of most of these species was normal with 8 bivalents at metaphase I with a few exceptions in which sporocytes showed 7II+2I. Pollen fertilities were high in most of the species studied with some exceptions.

Chromsome numbers of cultivars showed wide variations with $2n=16$ ($2x$), 24 ($3x$), 25 ($3x+1$), 31 ($4x-1$), 32 ($4x$) and 33 ($4x+1$). Karyotypes of these cultivars are also very complex and it is difficult to determine the parental species used for cultivar development. It was found that the *ligtu* hybrid definitely contained some unique chromosomes from *A. ligtu* species. Meiotic behaviors of chromosomes were abnormal in all cultivars, even in diploids. However, tetraploids ($2n=31$, 32, 33) showed fairly normal meiotic behavior with many bivalents and a few trivalents and univalents.

Pollen fertilities of cultivars are mostly correlated with meiotic behaviors: cultivars with very abnormal meiosis had very low pollen fertilities (4–8%), while the cultivars showing fairly normal meiosis had fairly good pollen fertility (60–70%).

ACKNOWLEDGEMENTS

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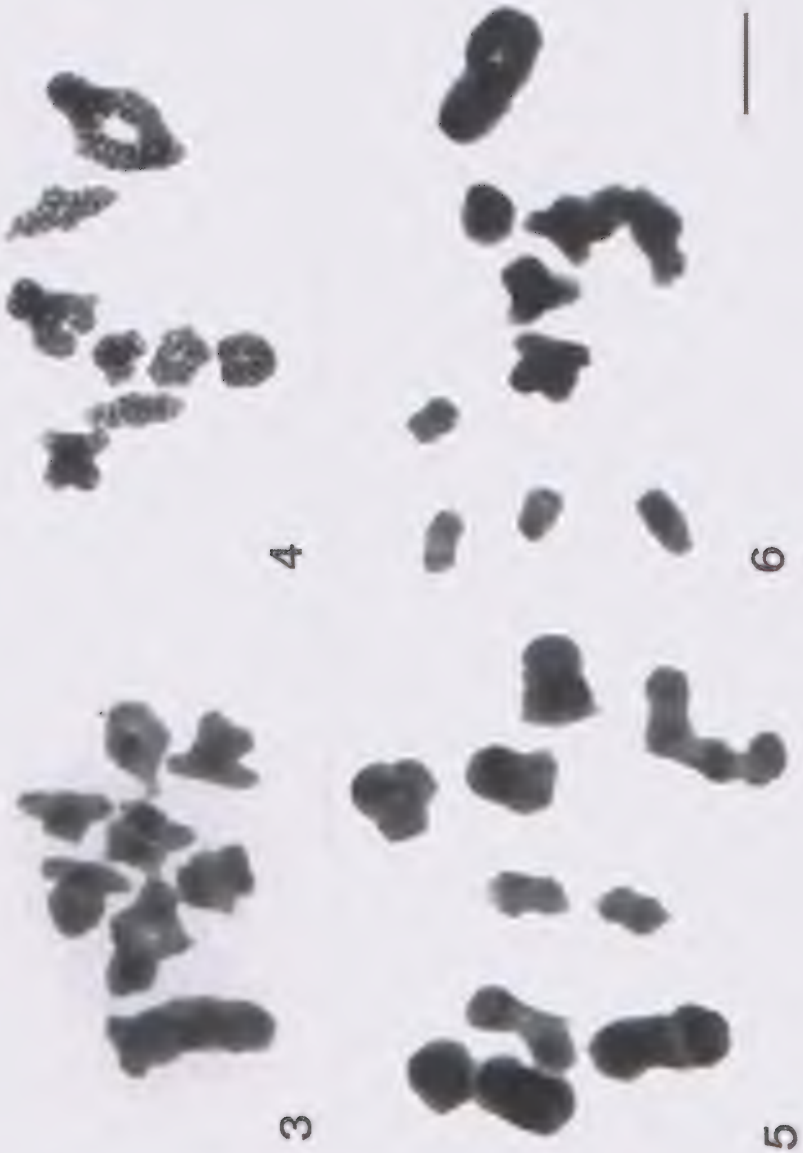
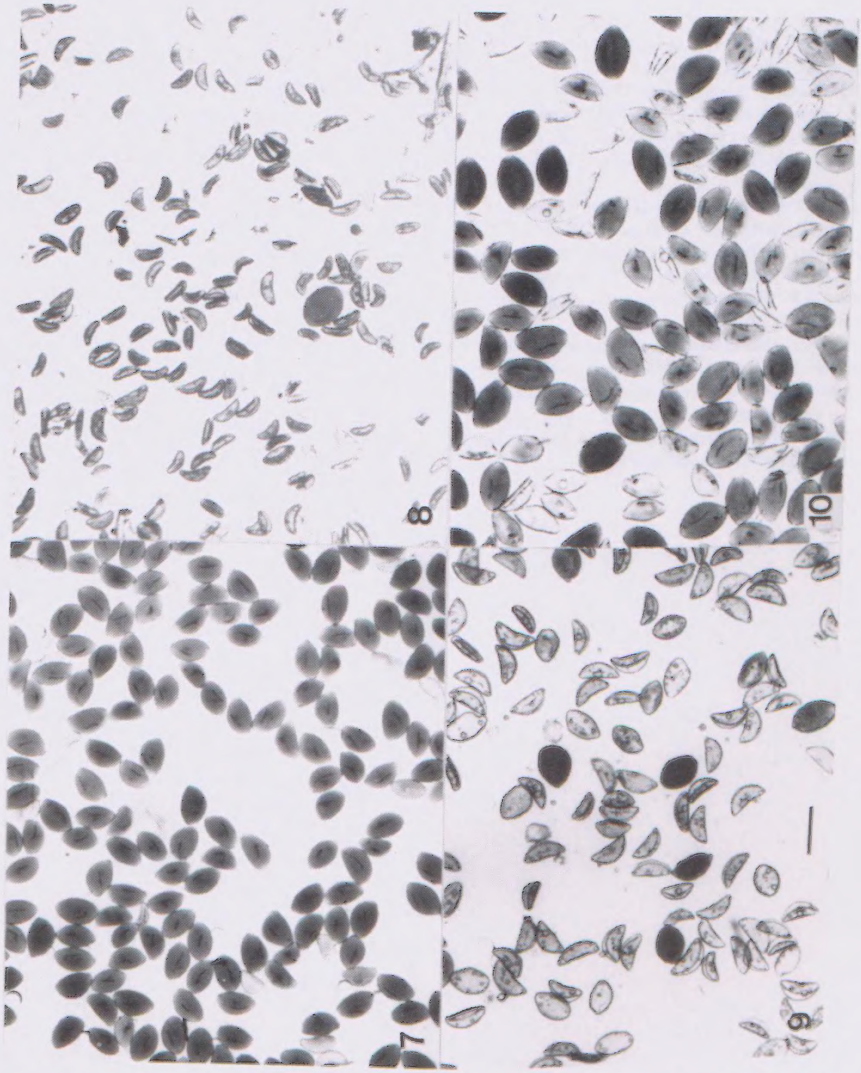


Figures 3–6. Meiotic metaphase I chromosomes in species and cultivars of *Alstroemeria*. 3, *A. aurantiaca* (2*n*=2*x*=16), 8 II. 4, *A. psittacina* (2*n*=16), 8 II. 5, *A.* cv. *ligtu* hybrid (2*n*=16), 8 II with a pair showing precocious separation. 6 *A.* cv. 'Orchid Fl.' (2*n*=16), 6II+4I.



Figures 7–10. Pollen fertility of two species and two cultivars in *Alstroemeria*. 7, *A. psittacina*. ($2n$=16). 8, *A.* cv. 'Canaria'. ($2n$=$2x$=16). 9, *A.* cv. 'Pink Triumph' ($2n$=$3x$=24). 10, *A.* cv. 'Jubilee' ($2n$=$4x$=32).

LITERATURE CITED

Broertjes, C. and H. Verboom. 1974. Mutation breeding of *Alstroemeria*. **Euphytica** 23:39–44.

Darlington, C.D. and A.P. Wylie. 1955. Chromosome Atlas of Flowering Plants. Allen and Unwin, London.

Hang, A. and T. Tsuchiya. 1988. Chromosome studies in the genus *Alstroemeria* II. Chromosome constitutions of eleven additional cultivars. **Plant Breeding** 100:273–279.

Lakshmi, N. 1976. Cytotaxonomic investigations in the genus *Alstroemeria*. **Chromosome Inf. Serv.** 20:20–21.

Rustanius, P.M. 1986. Karyotype analysis of *Alstroemeria ligtu* hybrids. M.S. thesis, Colorado State University, Fort Collins.

Sato, D. 1938. Karyotype alteration and phylogeny. IV. Karyotypes in Amaryllidaceae with special reference to the SAT-chromosome. **Cytologia** 9:203–242.

Strasburger, E. 1882. Uber den Teilungsvorgang der Zellkerne und das Verhaltnis der Kernteilung zur Zellteilung. **Arch. Mikr. Anat.** 21:476–596. (Cited from W.R. Taylor, 1926.)

Taylor, W.R. 1926. Chromosome morphology in *Fritillaria*, *Alstroemeria*, *Silphium*, and other genera. **Amer. Jour. Bot.** 13:179–193.

Tsuchyia, T. 1986. Chromosome engineering in ornamental flower breeding. **Garden Life** 1986 (12):55–58 (Japanese).

Tsuchyia, T. and A. Hang. 1987. Chromosome studies in genus *Alstroemeria*. **Acta Horticulturae** 205:281–287.

Tsuchyia, T., A. Hang, W.E. Healy and H. Hughes. 1987. Chromosome studies in the genus *Alstroemeria*. I. Chromosome numbers in 10 cultivars. **Bot. Gaz.** 148:519–524.

Whyte, R.O. 1929. Chromosome Studies I. Relationship of the genera *Alstroemeria* and *Bomarea* II. Interspecific hybrids in the genus *Nolana*. **New Phytol.** 28:319–344.